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Cover: Restoration of the cranium of *Hadronomus puckridgi*. Described and drawn by Dr. P.F. Murray.

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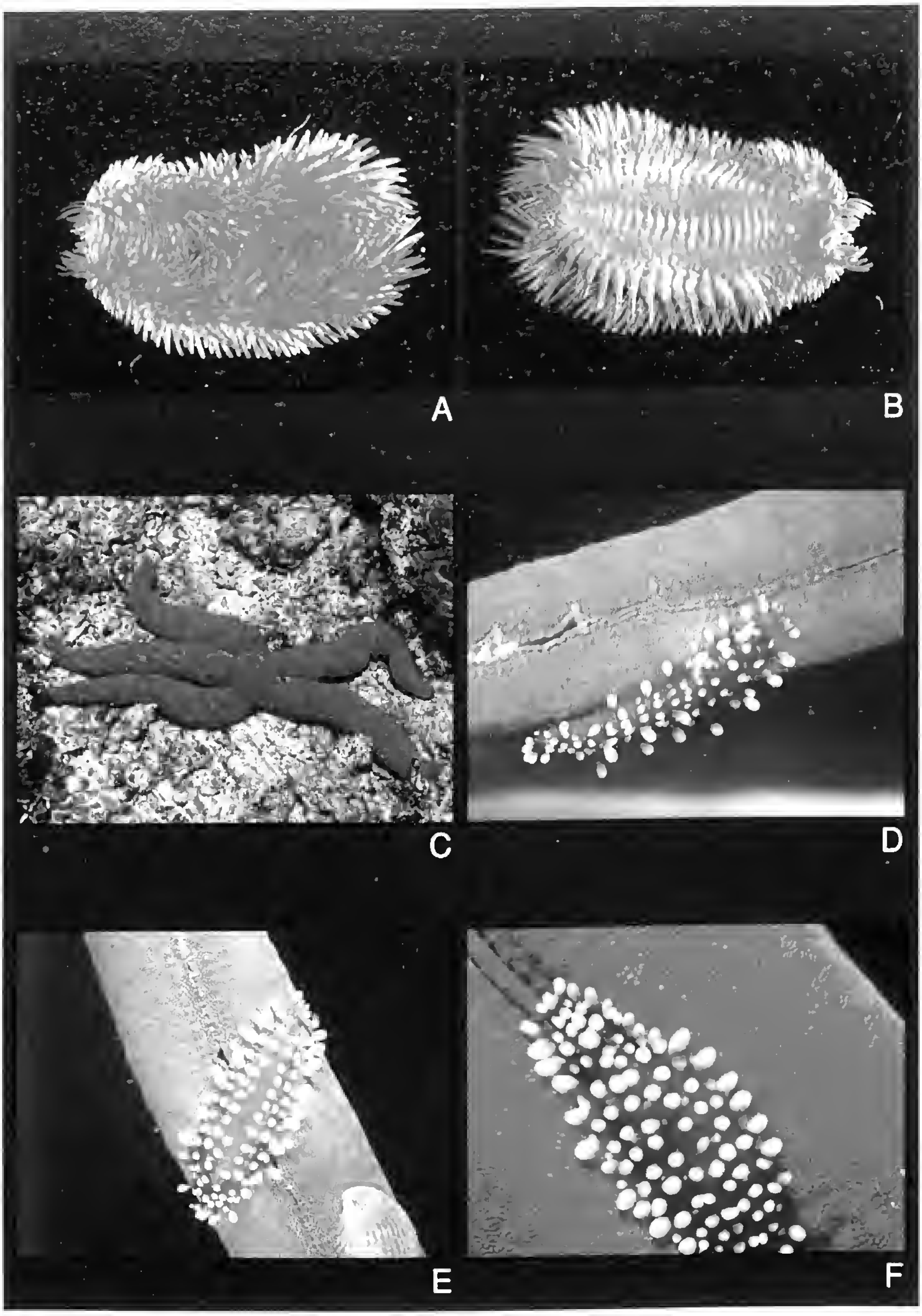

Polychaete worms. **A**, *Palmyra aurifera*, specimen from Reunion I. (ZUW A 2180), 15mm long, 8mm wide, 29 segments, dorsal view. **B**, ventral view of the same; **C**, The large blue starfish host, *Linckia laevigata*; **D-F**, *Asterophilia carlae* on the arm of its host. Note that when lying along the ambulacral groove the worm resembles protruding tube feet.

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SCIENCES

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REVISION OF THE SCALEWORM GENERA *ARCTONOE* CHAMBERLIN AND *GASTROLEPIDIA* SCHMARDA (POLYCHAETA: POLYNOIDAE) WITH THE ERECTION OF A NEW SUBFAMILY ARCTONOINAE.

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ABSTRACT

A new subfamily Arctonoinae is erected for several genera of polynoid scaleworms. Descriptions of *Arctonoe vittata* (Grube), *A. fragilis* (Baird), *A. pulchra* (Johnson) and *Gastrolepidia clavigera* Schmarda are provided. *Harmothoe tuberculata* Treadwell, 1906 is referred to *Bathynoe* Ditlevsen. A new genus and species *Asterophilia carlae* from Fiji and Indonesian waters is described.

KEYWORDS: Polychaeta, Polynoidae, *Arctonoe*, *Gastrolepidia*, new subfamily, new genus and species, generic revision, commensals, Indo-West Pacific.

INTRODUCTION

Pettibone (1953:8) divided the genera of polynoid scaleworms into three groups, based on the manner in which the lateral antennae were attached to the prostomium. These three groupings were: Lepidonotoid, where the ceratophores of the lateral antennae are attached directly to the anterior ends of the prostomium, appearing as outgrowths of the prostomium and represented by the subfamily Lepidonotinae Willey, 1902; Harmothoid, where the distinct ceratophores of the lateral antennae are attached to the ventral surface of the prostomium, represented by the subfamily Harmothoinae Horst, 1917 (=Polynoinae Muir, 1982); and a third group, Arctonoid, in which the ceratophores derive terminally or slightly ventrally from the prostomium and converge in the midline on the underside of the prostomium, represented by the genus *Arctonoe*.

Since then several other authors, notably Day (1967:41), and Uschakov (1977:33, 1982:60) have indicated that they view the arctonoid type of prostomium as a distinct one and that several genera possess its features. However, although many new subfamilies are now recognised in the family Polynoidae (Muir 1982; Pettibone 1976, 1983a, 1984, 1985a, 1985b; Uschakov 1977), there has been no attempt to assess the subfamily status of those genera which exhibit the arctonoid type of lateral antennae insertion, now widely described as subterminal, Day (1967) or terminoventral, Pettibone (1953).

The two genera *Arctonoe* Chamberlin, 1920 and *Gastrolepidia* Schmarda, 1861 have been considered by some authors to be closely related (Uschakov 1977; Pettibone pers. comm.). Both genera are revised here as part of a wider study of the systematics of the group of seven genera of polynoid scaleworms listed by Fauchald (1977) as possessing subterminal (terminoventral) insertion of the lateral antennae upon the distal end of the prostomium.

In this paper the similarities between *Arctonoe* and *Gastrolepidia* are confirmed and are considered sufficiently distinct from other polynoid scaleworms to warrant the erection of a new subfamily.

Several other genera are also referred to the new subfamily, including a new genus and species commensal on starfishes.

I wish to thank Dr Marian Pettibone for freely providing me with a great deal of unpublished information, including her diagnosis of Arctonoinae. I had independently arrived at the same conclusion regarding the need for a new subfamily for *Arctonoe* and *Gastrolepidia* but I found the information provided by Dr Pettibone especially useful in the construction of a subfamily description and the selection of genera to be placed within it. In deference to the important contribution she has made to this work, I have retained her

polynoid group name to be used for the subfamily.

The genus *Arctonoe* was originally established by Chamberlin, 1920 for his new species, *Arctonoe lia*. The type material bears the name *Schizonoe lia* which appears to have been a catalogue or manuscript name used by Chamberlin, and subsequently was changed by him to *Arctonoe lia* at the time of publication. The genus was monotypic until Hartman (1938:115-116) emended the genus *Arctonoe* and included four known species: *Polynoe vittata* Grube, 1855, *Polynoe pulchra* Johnson, 1897, *Lepidonotus fragilis* Baird, 1863, and *Harmothoe tuberculata* Treadwell, 1906.

Hartman considered that Chamberlin's *A.lia* was synonymous with the earlier published description of *Polynoe vittata*, and therefore the type species of the genus is now widely held to be *A. vittata*.

Gastrolepidia clavigera Schmarda, 1861 is monotypic. One other species *G. amblyphyllus* Grube, 1876, was synonymised with *G. clavigera* by Hartman (1959:70).

The following abbreviations are used in this paper to indicate the present location of material examined or discussed: AHF Allan Hancock Foundation, University of Southern California, Los Angeles; AM Australian Museum, Sydney; MCZ Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts; MNHN Museum National d'Histoire Naturelle, Paris; NMW Naturhistorisches Museum, Wien; NRS Naturhistoriska Riksmuseet, Stockholm; NTM Northern Territory Museum, Darwin; USNM National Museum of Natural History, Smithsonian Institution, Washington D.C.; VMM Victoria Memorial Museum, Ottawa; ZMA Zoologische Museum, Amsterdam; ZMH Zoologische Museum, Hamburg.

SYSTEMATICS

Family Polynoidae Malmgren, 1867
Subfamily Arctonoinae subfam. nov.

Diagnosis. Body usually elongated, with numerous segments. Elytra usually numerous pairs on segments 2, 4, 5, 7, then variable in arrangement. Prostomium bilobed, with three antennae, paired palps, and two pairs of eyes, on the posterior half of the prostomium. Anterior lobes of prostomium rounded, with or without small peaks; median antenna with large ceratophore in anterior notch; lateral antennae with distinct ceratophores inserted terminoventrally or ventrally, converging midventrally. Tentacular (first) segment not visible dorsally, tentaculophores lateral to prostomium, with acicula, achaetous, with two pairs of dorsal and ventral tentacular cirri resembling antennae. Second or buccal segment with or without nuchal lobe, with first pair of elytra, subbiramous parapodia, with ventral buccal cirri longer than following ventral cirri. Parapodia subbiramous, notopodia small, subconical, sometimes vestigial, on anterodorsal side of larger neuropodia, with notoacicula, notosetae usually few in number or absent; neuropodia deeply notched dorsally and ventrally, with rounded to pointed presetal lobes and shorter, rounded, postsetal lobes. Neurosetae relatively few, variable. Dorsal cirri on non-elytragerous segments, with cylindrical cirrophores posterodorsal to notopodia and distal styles; dorsal tubercles usually inconspicuous. Pygidium usually with pair of anal cirri. Pharynx usually with 9-11 pairs of papillae and 2 pairs of jaws. Often commensal.

Remarks. In the last 15 years the number of subfamilies in the family Polynoidae has been expanded from three to sixteen with one debatable addition (Table 1). This is remarkable since the status of the family Polynoidae has only recently gained wide acceptance. Only 21 years ago Day (1967) considered Polynoidae to be a subfamily of the family Aphroditidae. Although the recent proliferation of subfamilies suggests a dramatic change in the higher classification of the

Table 1. Sub families of *Polynoidae*

Sub family	*Author*
Iphioninae	Baird 1865
Lepidonotinae	Willey 1902
Harmothoinae	Horst 1917
Macellicephalinae	Hartmann-Schröder 1971
Bathyedithinae	Pettibone 1976
Polaruschakovinae	"
Macelloidinae	"
Macellicephaloidinae	"
Bathymacellinae	"
Admetellinae	Uschakov 1977
Polyodontinae	Muir 1982
Gesiellinae	"
Lepidonotopodinae	Pettibone 1983a
Branchipolynoinae	Pettibone 1984
Branchiplicatinae	Pettibone 1985a
Branchinotogluminae	Pettibone 1985b
Lepidastheniinae	Pettibone 1989b

polynoid scaleworms, earlier authors did recognise the presence of distinct groupings within the polynoid scaleworms irrespective of whether they considered the Polynoidae to be a subfamily or a family. Once the status of Polynoidae as a family was widely accepted, the elevation of most of these groupings to subfamily status was inevitable.

The three oldest subfamilies Iphioninae Baird, 1865, Harmothoinae, and Lepidonotinae, included all of the polynoid scaleworms until Hartmann-Schröder erected Macellicephalinae in 1971.

The majority of polynoid scaleworms have remained in the two large subfamilies Harmothoinae and Lepidonotinae. The new subfamilies which have been erected by Pettibone (1976, 1983a, 1984, 1985a,b, 1989a) and Uschakov (1977) contain polynoid species mostly from deep water and hydrothermal vents. The criteria for erection of new subfamilies for this deep water fauna are the presence of unusual morphological features not found on species of scaleworms in existing subfamilies (e.g. branchiae) and the absence of other features common among polynoid worms, such as a reduction in the number of antennae on the prostomium.

Muir (1982:174) erected a new subfamily Gesiellinae for *Gesiella* Pettibone, 1976, a genus with unusual accessory filamentous sensory organs. Muir also reduced Polyodontidae to subfamily level within the Polynoidae as the only difference between polyodontids and polynoids is the presence of spinning glands in the polyodontids. This has not been followed by Pettibone (1989b) in her revisionary study of the family Acoetidae Kinberg (=Polyodontidae Augener).

Therefore in spite of the creation of these new subfamilies the majority of polynoid scaleworms are still placed in either Lepidonotinae or Harmothoinae. The new subfamily Arctonoinae represents a group of genera which share a suite of morphological features which are not shared by other genera in Lepidonotinae or Harmothoinae. These features are indicated in the diagnosis of the subfamily.

Apart from *Arctonoe*, *Gastrolepidia*, *Bathynoe* Ditlevsen, 1917, and *Asterophilia*, a new genus covered in this paper, I would also include the following genera: *Adyte* Saint-Joseph, 1899; *Paradyte* Pettibone, 1969a; *Subadyte* Pettibone, 1969a; *Pottsiscalisetosus* Pettibone, 1969a; *Australaugeneria* Pettibone, 1969a; *Hololepidella* Pettibone, 1969b, *Neohololepidella* Pettibone, 1969b; *Parahololepidella* Pettibone, 1969b; *Minisculisquama* Pettibone, 1983b; *Disconatis* Hanley and Burke, 1988.

Previously, (Hanley 1984) I have followed Muir (1982), and Tebble and Chambers (1982) in synonymising *Paradyte* and *Subadyte* Pettibone, 1969a with *Adyte* Saint-Joseph, 1899. Since then I have examined a lot more material and I now consider Pettibones' erection of these two genera to be valid.

It is important to note that a large number of the species in the genera listed above are commensals, predominantly with echinoderms. While it may be argued that these species may have acquired the commensal lifestyle independently, the great similarities of morphology of prostomium, parapodia, and setae suggest that all may have a common ancestor which was a commensal.

Genus *Arctonoe* Chamberlin

Arctonoe Chamberlin, 1920:6B (type species *Arctonoe lia* Chamberlin, 1920, by original designation. Referred to *Arctonoe vittata* by Hartman (1938:116). Gender feminine).

Halosydnoides Seidler, 1924:134 (type species *Polynoe vittata*, herein designated. Referred to genus *Arctonoe* by Hartman (1938:116). Gender feminine).

Diagnosis. Body elongated, flattened, with numerous segments (100 and more) tapering posteriorly. Elytra and prominent elytrophores, numerous pairs on segments 2, 4, 5, 7, alternate segments to 21, 23, 26, 28, 29, 31, 33, continuing on alternate segments to end of body, sometimes irregular sequence and\or asymmmetrical - elytron and dorsal cirrus on same segment. Elytra soft, translucent, without tubercles or papillae. Prostomium bilobed, without cephalic peaks, with two palps and three antennae with distinct ceratophores. Median antenna inserted in anterior notch; lateral antennae inserted terminoventrally with ceratophores converging midventrally. Two pairs of eyes, similar in size, lying close to each other on posterior half of the prostomium. First or tentacular segment not visible dorsally, tentaculophores lateral to

prostomium, achaetous, with two pairs of tentacular cirri, facial tubercle absent. Second or buccal segment with or without dorsal nuchal fold, with first pair of elytra on prominent elytrophores, subbiramous parapodia and ventral buccal cirri longer than following ventral cirri. Pharynx large, muscular, distally nine pairs of soft papillae encircling mouth and two pairs of chitinous jaws. Parapodia subbiramous, notopodia short, subconical; neuropodia larger, deeply incised distally with well developed presetal and postsetal lobes. Notosetae short, serrated with notched indented tips. Neurosetae longer, stouter, straight or hooked distally. Dorsal cirri with cylindrical cirrophore and distal styles. Dorsal tubercles moderately to well developed. Ventral cirri short, tapering to filiform tip, sometimes vestigial posteriorly. Nephridial papillae well developed, beginning on or about segment 6, continuing to end of body. Anus terminal, no anal cirri.

Commensal with echinoderms, molluscs, and other polychaetes.

Distribution. Northern and north-eastern Pacific Ocean.

Remarks. According to Chamberlin's original description of *Arctonoe* the elytra occur on segments "2, 4, 5, 7, 9, etc" whereas the correct arrangement is alternation on odd numbered segments of the body to 23, 26, 28, 29, 31, 33 and thereafter on alternating segments, but with some variability posteriorly including asymmetry, i.e. an elytron on one side of a segment and a dorsal cirrus on the other. This variability was first mentioned by Hartman (1938:115) and later endorsed by Pettibone (1953:56), and Uschakov (1982:116).

Seidler (1924) referred *Polynoe vittata* to a new genus *Halosydnoides*. However, the synonymy of *Arctonoe lia* with *Polynoe vittata* by Hartman (1938:116) means that Chamberlin's name *Arctonoe* has priority as the correct generic name.

Arctonoe vittata (Grube)
(Figs 1A-F, 2A-L, 3A-H)

Polynoe vittata Grube, 1855:82,83.

Acholoe vittata - Marenzeller 1902:576, Taf. III Fig. 13.

Halosydnoides vittata - Seidler 1924:134, 135; Monro 1928:312; Okuda 1936:565-568, Figs 4, 5.

Arctonoe vittata Hartman 1938:116; 1939:29, 30, Pl. 3 Figs 33-37; 1944:244; 1948:6, 11, 12, Fig. 2a-f; 1956:252, 260, 265; 1968:49; Berkeley and Berkeley 1941:23-24; 1942:188; 1948:20, 21, Figs 24, 25; Skogsberg 1942:489-497, Figs B-D; Hartman and Reish 1950:6; Pettibone 1953:57-61, Pl. 28 Figs 251-258, Pl. 29 Figs 259-271; Uschakov 1955:132, Fig. 23E,F; 1982:221, 223, Pl. XXXV Figs 1-7; Khlebovich 1961:166; Imajima and Hartman 1964:19; Buzhinskaja 1967:82; Banse and Hobson, 1974:26.

Lepidonotus lordi Baird, 1863:107.

Halosydna lordi - Baird 1865:190, 191; Moore 1908:330; Treadwell 1914:181; 1926:1; Chamberlin 1920:9B; Berkeley 1923:212.

Polynoe lordi - Johnson 1897:175-177, Pl. 7 Figs 35, 44, Pl. 8 Fig. 51; 1901:388-390; Treadwell 1923:4.

Halosydna succiniseta Hamilton, 1915: 234.

Arctonoe lia Chamberlin, 1920:6B, 7B, Pl. I Figs 1-4, Pl. II Figs 1-3; Annenkova 1937:146,147; 1938:131.

Halosydnoides lia - Annenkova 1934:322.

Type material. PARATYPES of *Arctonoe lia* - MCZ 2190, 2191a, Grantley Harbour, Teller, Alaska, station 20b-c, 30.vii.1913, 2-3 fathoms, sandy bottom; MCZ 2191, Point Clarence, Alaska, station 20g, 4.viii.1913, 2-3 fathoms, mud; VMM 16-56 (cat no. 29, or 27, 28), Port Clarence, Alaska, station 20g, 4.viii.1913, 2-3 fathoms, F. Johansen.

Additional material. AHF N6706, Northern California, from *Diadora aspera*, 4 specimens.

Description. Body flattened, widest part of body about 1/3 from head, tapering rapidly anteriorly, gradually posteriorly, fragile. Length 12-50mm, width 3-7mm. Numerous body segments (36-80). Dorsal and ventral surfaces of body variably pigmented. Some specimens (AHF) with light, streaky brown transverse bands across dorsal surface, and one broad brown band on segment 8. Pigmentation of specimens varying considerably according to host (Pettibone 1953).

Numerous pairs of large, soft, smooth elytra attached on segments 2, 4, 5, 7, 9, alternate segments to 23, 26, 28, 29, 31, 33, thereafter attachment pattern varying between specimens, usually on alternating segments to end of body but with some elytra on consecutive segments and often asymmetrical. Variation

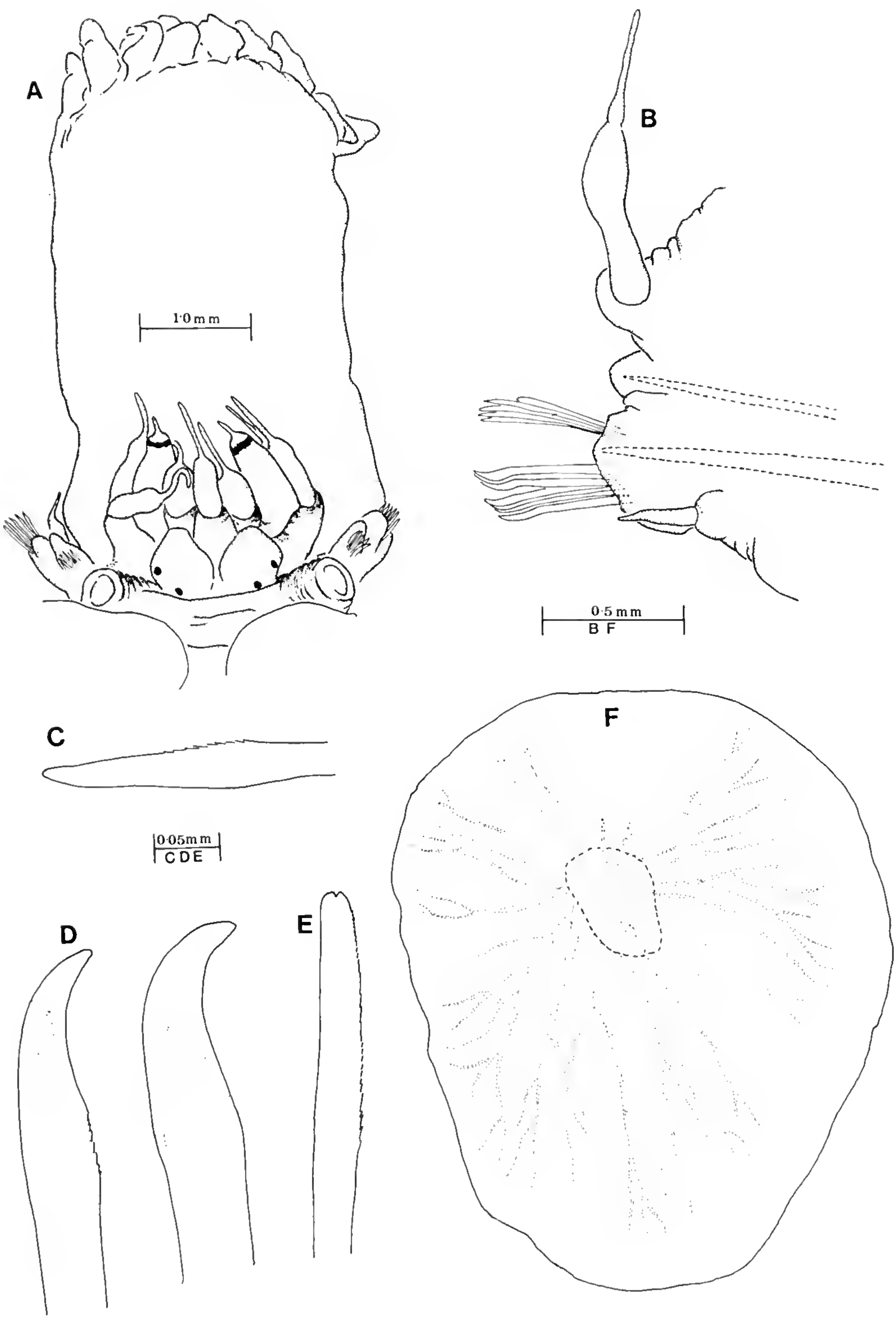

Fig. 1. *Arctonoe vittata* AHF N6706, large gravid female : **A**, anterior end; **B**, cirrigerous parapodium from 36th segment; **C**, lower neuroseta; **D**, middle neurosetae; **E**, upper neuroseta; **F**, elytron.

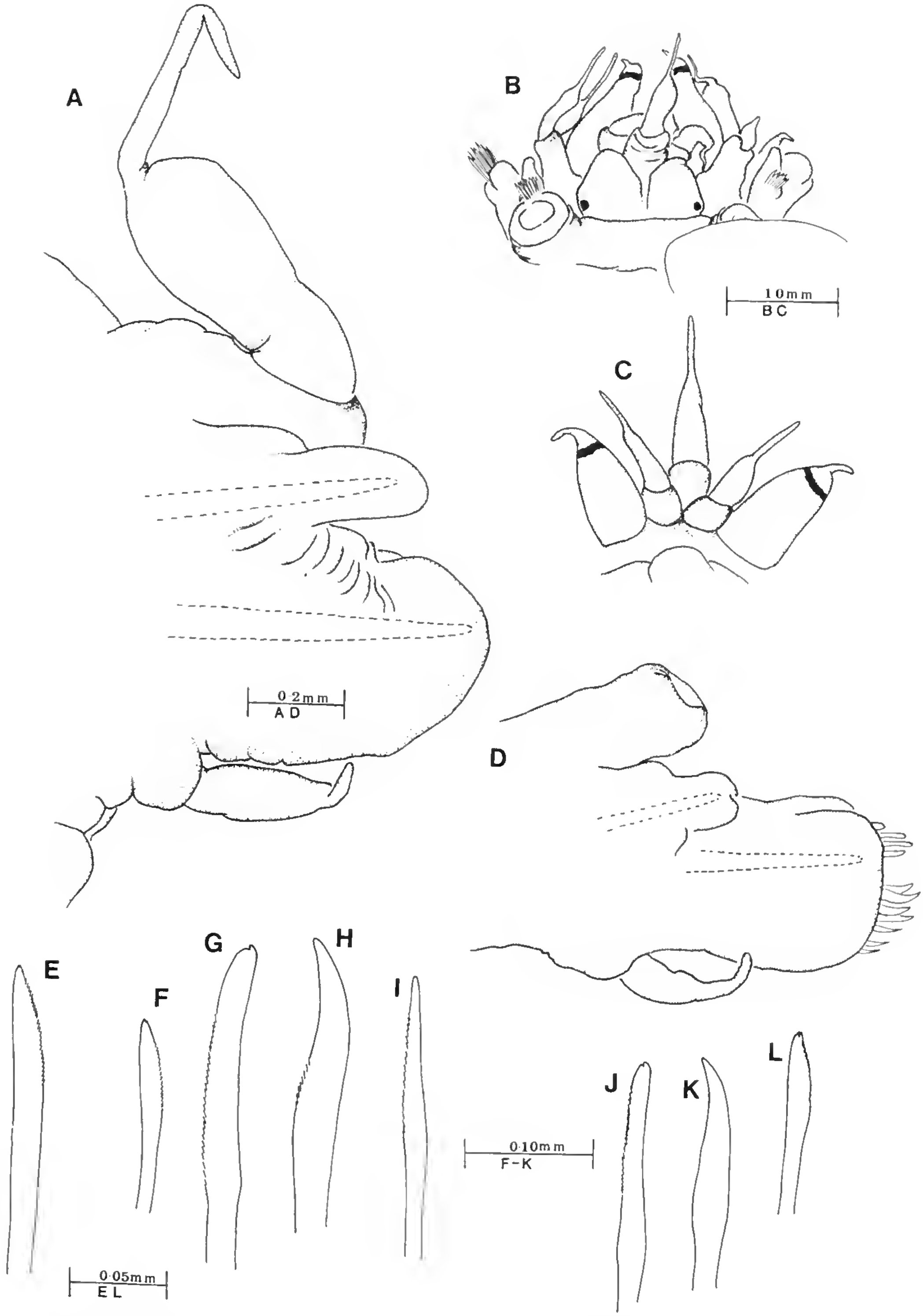

Fig. 2. *Arctonoe vittata* AHF N6706, large gravid female: **A**, cirrigerous parapodium from 3rd segment, anterior view; **E, F**, notosetae from same; **G**, upper neuroseta; **H**, middle neuroseta; **I**, lower neuroseta. AHF N6706, smaller specimen: **B**, anterior end, dorsal view; **C**, ventral view of prostomium; **D**, cirrigerous parapodium from 3rd segment, anterior view; **J**, upper neuroseta; **K**, middle neuroseta; **L**, notoseta.

Table 2. Variation in elytron attachment pattern on specimens of *Arctonoe vittata*

Specimen	*Length*	*Width*	*No. of segments*	*Elytra attached on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 28, 29, 31, 33, and thereafter on segments.*	*No. of elytra pairs*
A. lia paratype VMM	12.3mm	3.2mm	45	35, 37, 39, 41, 43, 45	23
A lia paratype MCZ	22.4mm	3.5mm	55	35, 37, 39, 41, 43, 45, 48, 50, 52, 54 left side 35, 37, 39, 41, 43, 45, 47, 50, 52, 54 right side	27
A. lia Type VMM	15mm	3.0mm	52	35, 37, 39, 41, 43, 45, 47, 49, 51	26
AHF N6706 (3)	48mm	6.0mm	76	35, 37, 39, 41, 43, 45, 47, 49, 51, 53, 55, 57, 59, 61, 63, 65, 67, 69, 71, 73, 75 left 34, 35, 37, 38, 39, 41, 43, 45, 47, 49, 51, 53, 55, 57, 59, 61, 63, 65, 67, 69, 71, 73, 75 right	39 left 41 right
AHF N6706 (2)	35mm	4.0mm	63	35, 37, 39, 41, 43, 45, 47, 49, 51, 53, 55, 57 34, 36, 38, 40, 42, 44, 46, 48, 50, 52, 54	30 left 29 right
AHF N6706 (1)	50mm	6.7mm	80	35, 37, 39, 41, 43, 45, etc, alternating to 75, 77, 79	40
AHF N6706 (4)	32mm	–	64	35, 37, 38, 40, 42, etc. alternating to 60, 62, 64	33

of elytral attachment pattern on the specimens examined is given in Table 2.

Elytra without tubercles, fringe of papillae, or frilled margins (Figs 1F, 3E). Elytra overlap each other posteriorly and first pair overlapping medially hiding prostomium but rest of dorsum exposed medially.

Prostomium bilobed, much wider than long, without cephalic peaks (Figs 1A, 2B, 3A). Two pairs of eyes, anterior pair small, lying dorsolaterally just behind widest point of prostomium, posterior pair lying dorsally close behind first pair, lying slightly closer to midline. Palps, short, stout with abruptly tapered tips. Three antennae. Median antenna with large cylindrical ceratophore inserted in anterior notch, style smooth, basally cylindrical, with subterminal inflation (sometimes not well defined) and a relatively long filiform tip. Lateral antennae with distinct ceratophores shorter and thinner than median ceratophore, inserted terminoventrally on prostomium (Figs 1A, 2B, 3A) and converging midventrally (Figs 2C, 3C), styles similar to median style but shorter.

Tentacular (first) segment achaetous, not visible dorsally, tentaculophores lateral to prostomium, two pairs of dorsal and ventral tentacular cirri, with smooth styles, similar in length and shape to style of median antenna. Facial tubercle very weakly developed. Segment 2 without nuchal fold, with first pair of elytra, subbiramous parapodia, notosetae, neurosetae, and ventral buccal cirri longer than following ventral cirri.

Parapodia subbiramous (Figs 1B, 2A,D, 3B,D). Notopodium small, subconical, on anterodorsal face of large neuropodium. Anterior notopodia well developed, becoming less so posteriorly, particularly on large specimens. Neuropodium deeply cut dorsally and ventrally (Figs 1B, 2A,D, 3B,D) with rounded presetal lobe and slightly shorter, rounded postsetal lobe. Dorsal cirrophores on segments without elytra, large, cylindrical, styles basally cylindrical, with subterminal inflation and long filiform tip. Ventral cirri short, basally inflated with long filiform tip. Nephridial papillae well developed, beginning on segments 6-12, continuing to end of body.

Notosetae (Figs 2E,F,L, 3F) short, curved slightly, with notched tips and rows of serrations. Notosetae decreasing in number posteriorly on smaller specimens and often absent from all but a few anterior segments on larger specimens. Neurosetae longer, larger, than notosetae, present on all segments, with subdistal swelling, upper ones with prominent rows of serrations (Figs 1E, 2G,J, 3H) and notched tips, middle and lower ones (Figs 1C,D, 2H,I,K, 3G) with very faint rows of serrations and strongly curved unidentate tips (often broken); neurosetae in middle of bundle intermediate between the two extremes.

Pygidium small, anus terminal, anal cirri absent.

Commensal on or with wide variety of echinoderms, molluscs, and polychaetes.

Distribution. North Pacific: Japan, Kurile Islands, Okhotsk and Bering Seas, Alaska south to California and Ecuador.

Remarks. The location of the type specimen/s of *Polynoe vittata* is unknown. Most of the material described by Grube is housed in the Naturhistorisches Museum in Berlin.

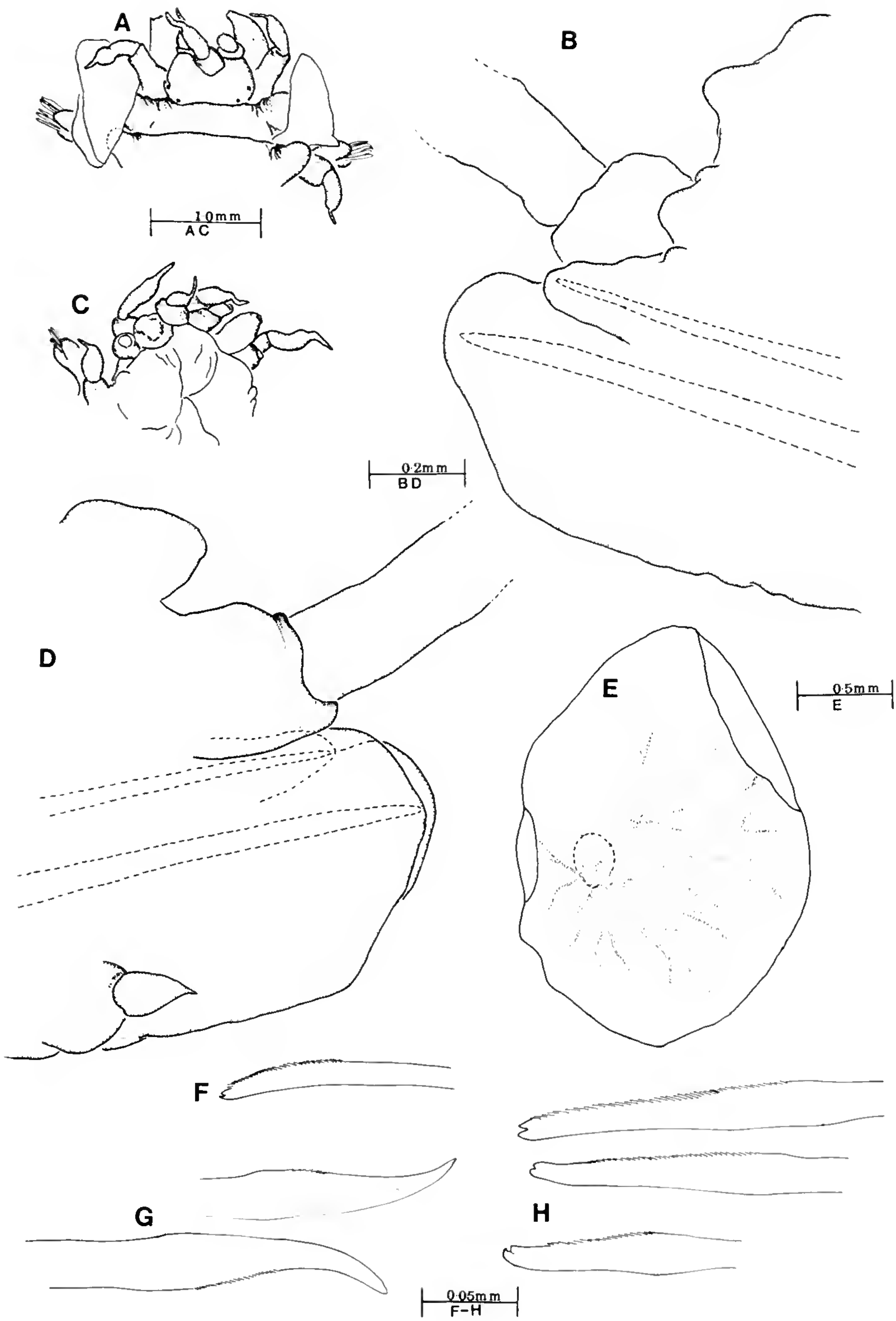

Fig. 3. *Arctonoe vittata* (paratype of *Arctonoe lia* Chamberlin) MCZ 2191: **A,** anterior end, dorsal view; **B,** anterior cirrigerous parapodium, anterior view; **C,** ventral view of anterior end; **D,** anterior cirrigerous parapodium, posterior view; **E,** right 4th elytron from segment 7; **F,** notoseta; **G,** middle neurosetae; **H,** upper neurosetae.

However correspondence with Dr. G. Hartwich indicates there is no type material of this species in that Institution. Several types of species erected by Grube are held in the Wroclaw Museum, Poland, listed in Wiktor (1980), but the type of this species is not among them.

The original description of *Polynoe vittata* by Grube (1855) mentions that the elytra are smooth, soft and found on segments 2, 4, 5, and alternating segments to 26, 28, 29, 31, and then on alternating segments to the end of the body. The description of elytron arrangement up to segment 31 agrees well with subsequent descriptions of specimens referred to this species. In addition Grube describes the notosetae as small, blunt tipped, with rows of fine serrations and states they are few in number or absent altogether on most specimens. He describes the neurosetae as much larger than the neurosetae with lanceolate tips, the upper ones with rows of serrations, the lower ones unidentate and with slightly curved tips. Therefore the original description is sufficient to allow discrimination between this species and the very similar *A. pulchra* which does not have two forms of neurosetae.

The paratypes of *A. lia* are in poor condition, all having been dry for some period of time and therefore distorted with most appendages such as cirri and antennae missing. However the pattern of elytron attachment is consistent with that documented here and elsewhere for the genus *Arctonoe* and all the paratypes possess the two forms of neurosetae described by Grube so I have no hesitation in supporting the synonymy of *A. lia* with *A. vittata*, as first proposed by Hartman (1938).

Unfortunately the type of Baird's *Lepidonotus lordi* must be considered lost as it is not in the collection of the British Museum of Natural History (Alex Muir pers.comm.). The original description of this species (Baird 1863) is poor, particularly as it gives no clue to the pattern of elytron attachment and it does not adequately describe the setae. A later description of the species by Baird (1865) as *Halosydna lordi*, is more useful as it describes the presence of two forms of neurosetae, similar to those described for *A.vittata* by Grube. Other features described by Baird, which lend credence to the synonymy of *L. lordi* with *A. vittata*, are the colour pattern of the specimens, the numerous pairs of elytra, and the association of all the specimens with the mollusc *Fissurella cratitia*, a known host of *A. vittata*.

In the paper describing *A. lia*, Chamberlin (1920) also mentions a specimen of *Halosydna lordi* , and so obviously did not consider it synonymous with his own species. He provides a record of one specimen and claims that its distinctive colour pattern suggests it should be referred it to *H.lordi*; one can only assume in the absence of a comprehensive description that he did not examine this specimen closely, so this record should be regarded with some suspicion.

Arctonoe fragilis (Baird)
(Figs 4A-F, 5A-F)

Lepidonotus fragilis Baird, 1863:108.

Halosydna fragilis - Baird 1865:191, 192; Berkeley 1923:212; 1924:193.

Polynoe fragilis - Johnson 1897:179-181, Pl.VII, Figs 36, 45, Pl.VIII, Figs 52, 52a; 1901:390; Moore 1908:332; Treadwell 1914:181.

Acholoe fragilis - Hartman 1936:32.

Arctonoe fragilis - Hartman 1938:116; 1944:244; 1948:11; 1968:45, Figs 1-3; Berkeley and Berkeley 1942:188; 1948:20, Fig. 23; Hartman and Reish 1950:6; Pettibone 1953:64-66, Pl. 31, Figs 281-290; Banse and Hobson 1974:26; Uschakov 1982:116.

Material. AHF N10, outer side of Tamales Point, California, 9.vi.1941, commensal in ambulacral groove of *Pisaster giganteus*, 2 specimens.

Description. Body large, flattened, elongate, widest about 1/3 from anterior end, tapering rapidly anteriorly, more gradually posteriorly. Numerous segments (up to 100). The smaller of the two specimens is 23mm, the larger specimen 50mm in length. The width, including parapodia, of smaller specimen is 2.5mm, and the width of the larger specimen is 5mm. Dorsal and ventral surfaces of body without pigmentation (due to preservation), live animals tending to match coloration of host (Pettibone 1953).

Numerous pairs of large, soft, smooth elytra attached on segments 2, 4, 5, 7, 9, alternate segments to 23, 26, 28, 29, 31, 33, thereafter attachment pattern varies between specimens, usually on alternating segments to end of body but with some elytra on consecutive segments and sometimes asymmetrical. On

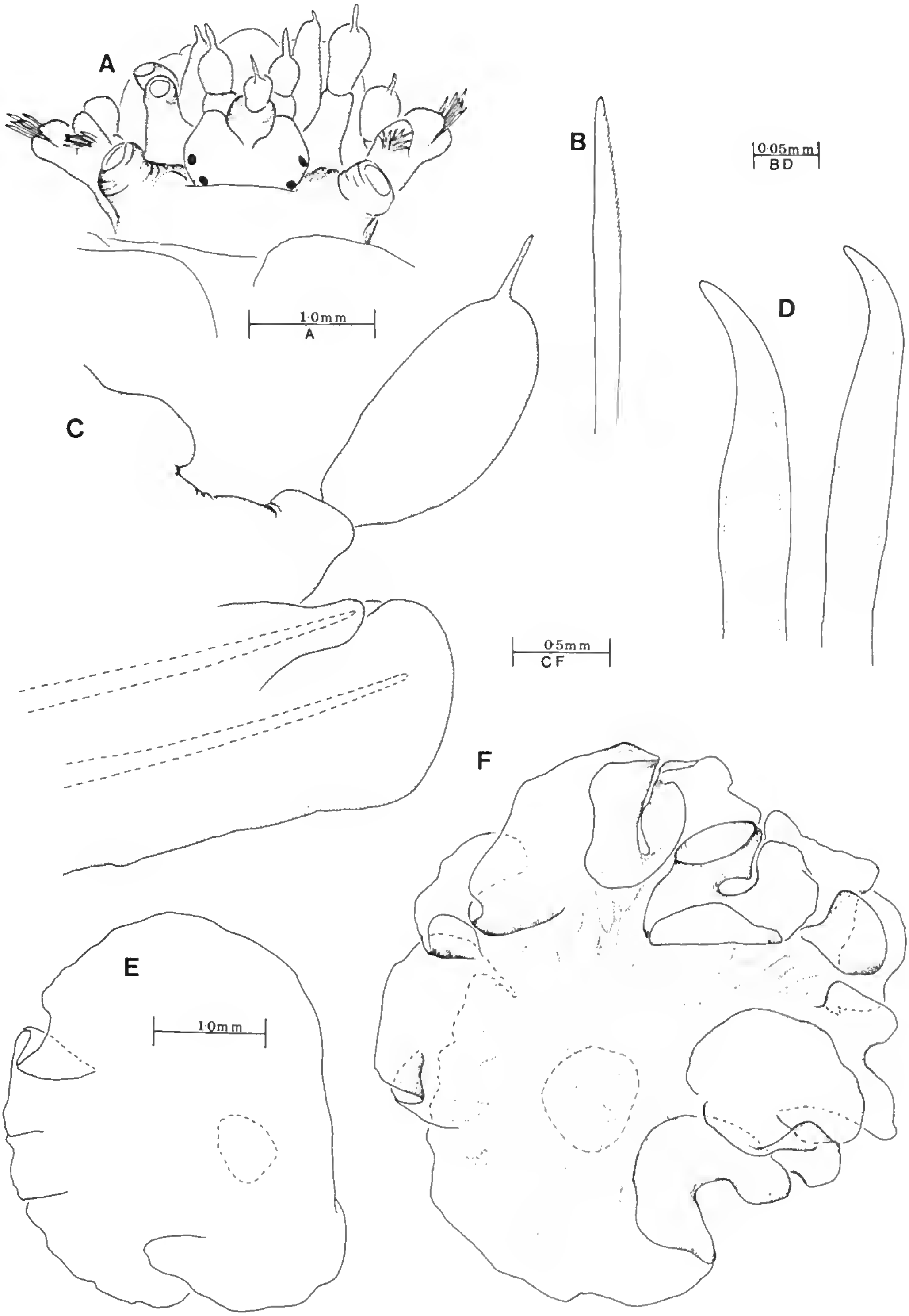

Fig. 4. *Arctonoe fragilis* AHF N10, large specimen: **A,** anterior end, dorsal view; **B,** notoseta; **C,** parapodium from segment 12, anterior view; **D,** neurosetae; **E,** posterior elytron; **F,** anterior elytron.

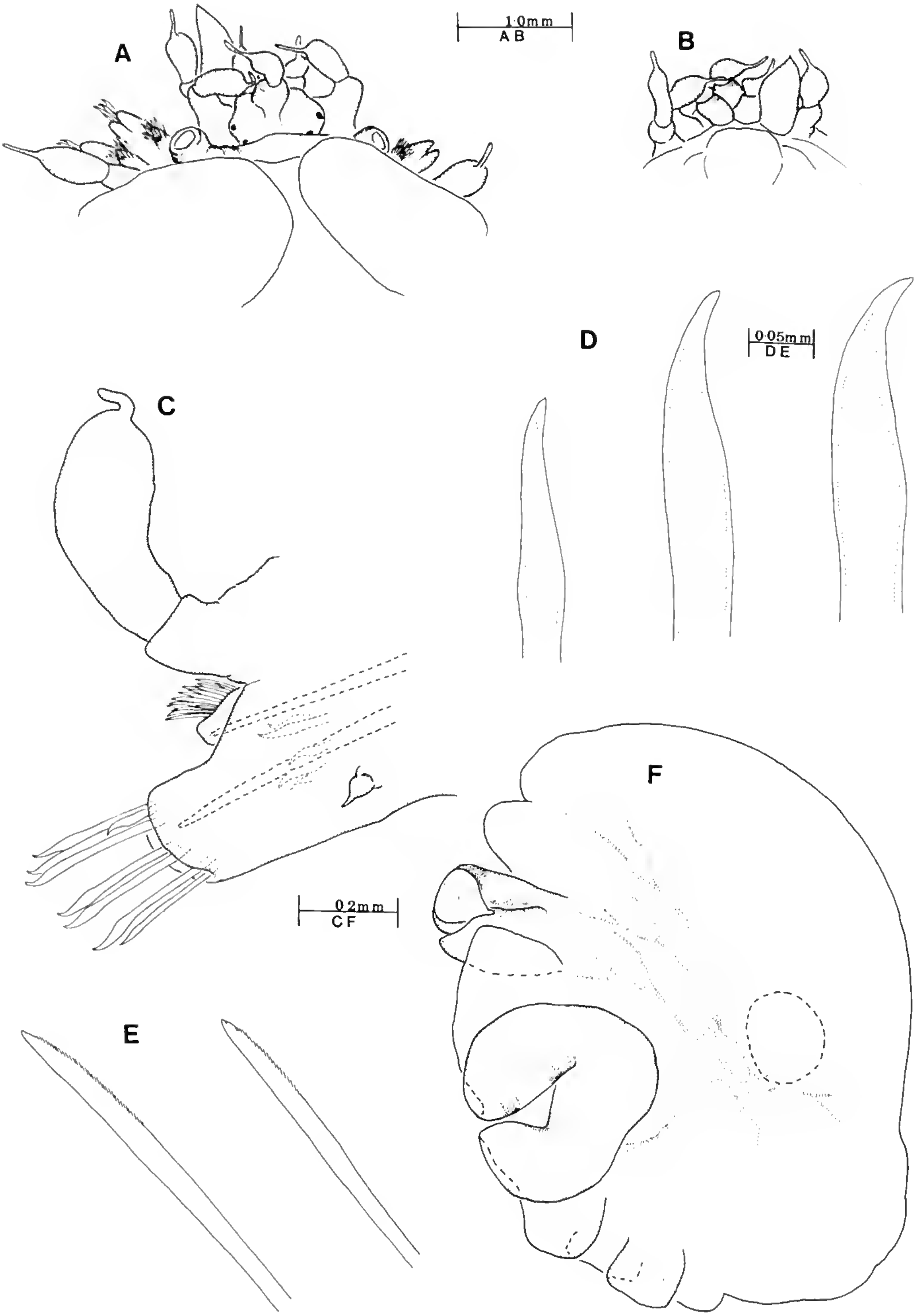

Fig. 5. *Arctonoe fragilis* AHF N10, small specimen: **A,** anterior end, dorsal view; **B,** ventral view of anterior end; **C,** posterior view of cirrigerous parapodium from segment 12; **D,** neurosetae; **E,** notosetae; **F,** anterior elytron.

smaller of two specimens examined, elytra on segments 35, 37, 39, 41, 43, 45,and 47. On large specimen elytra on segments 35, 37, 39, 40, 42, 44, 46, 48, 50, 51, 53, 55, and 57 on left side, and on right side on segments 34, 36, 38, 40, 42, 44, 46, 48, 50, 52, 54, 56, 58, and 60. Elytra (Figs 4E,F, 5F) without tubercles or fringe of papillae, with margin conspicuously convoluted and folded (frilled), particularly on anterior elytra, becoming less so posteriorly. Elytra overlapping each other posteriorly but not in midline, thus exposing prostomium and dorsum exposed medially.

Prostomium bilobed, much wider than long, without cephalic peaks (Figs 4A, 5A). Two pairs of eyes, anterior pair small, lying dorsolaterally at the widest part of the prostomium, posterior pair similar size, lying relatively close behind first pair, closer to midline. Palps, short, stout, with abruptly tapered, short, filiform tips. Median antenna with large cylindrical ceratophore inserted in anterior notch, style smooth, short, basally inflated with relatively long filiform tip. Lateral antennae on distinct ceratophores shorter and thinner than median, inserted terminoventrally on prostomium (Fig. 5B), converging midventrally, antennae similar in shape to median antenna but slightly shorter.

Tentacular (first) segment, not visible dorsally, large tentaculophores lateral to prostomium, achaetous, with two pairs of tentacular cirri, smooth, basally cylindrical, with prominent subterminal inflation and long filiform tip, similar in length or longer than median antenna. Facial tubercle poorly defined. Segment 2 without nuchal fold, with first pair of elytra, subbiramous parapodia, and long ventral buccal cirri.

Parapodia subbiramous (Figs 4C, 5C). Notopodium small, subconical, with notoacicula, on anterodorsal face of much larger neuropodium. Neuropodium short, blunt, deeply cut dorsally (Fig. 4C, 5C), with presetal lobe bluntly rounded, acicula does not protude, postsetal lobe shorter, rounded. Cirrophores of dorsal cirri on segments without elytra, large, cylindrical, styles thick, with large subdistal inflation abruptly tapering to filiform tip (Figs 4C, 5C). Ventral cirri vestigal, button-like after first few segments. Nephridial papillae conspicuous on one specimen from segment 6 to end of body.

Notosetae (Figs 4B, 5E) short, thin, not curved, slender tips, sometimes notched, with rows of fine serrations. Neurosetae (Figs 4D, 5D), longer, stout, with subdistal swelling, tips sharply tapered, strongly hooked, some with fine serrations, relatively few neurosetae present on each segment, some newly formed ones visible inside parapodia.

Pygidium small, inconspicuous, anus terminal, anal cirri not evident. Pharynx not everted. Commensal with asteroids.

Distribution. North-eastern Pacific: Alaska to central California.

Remarks. The type specimen/s of *Lepidonotus fragilis* are not in the British Museum of Natural History (Alex Muir pers. comm.). The original description is also deficient in several respects (admitted by Baird). In particular, there is no mention of the number of pairs of elytra or their arrangement, although this is because the worms were fragmented (their fragile condition is reflected in the species name), and there is no mention of frilled margins on the elytra.

The characteristic which has allowed subsequent authors to ascribe specimens to Baird's species is the reduction of the ventral cirri to rudimentary knobs, particularly on the posterior segments of the body, a characteristic described by Baird. Another feature which has been useful in referring specimens to Baird's species is its association with asteroids.

The specimens examined here and the descriptions provided by subsequent authors agree for the most part with the original description. However one significant discrepancy is Baird's description of the notosetae as "short, straight and simple, not toothed or serrate on the edges" (Baird 1863). All the specimens I have examined, and those that have been previously referred to this species, have notosetae which are serrated and have notched tips. The status of this species could therefore be considered to be doubtful, except that there are no other species known which have the features of rudimentary ventral cirri, commensal on starfishes, northeastern Pacific distribution and fragile body.

Arctonoe pulchra (Johnson)
(Figs 6A-F, 7A-H)

Polynoe pulchra Johnson, 1897:177-179, Pl.VII, Figs 34, 43, 43a, Pl.VIII, Figs 50, 50a, 50b; 1901:390.

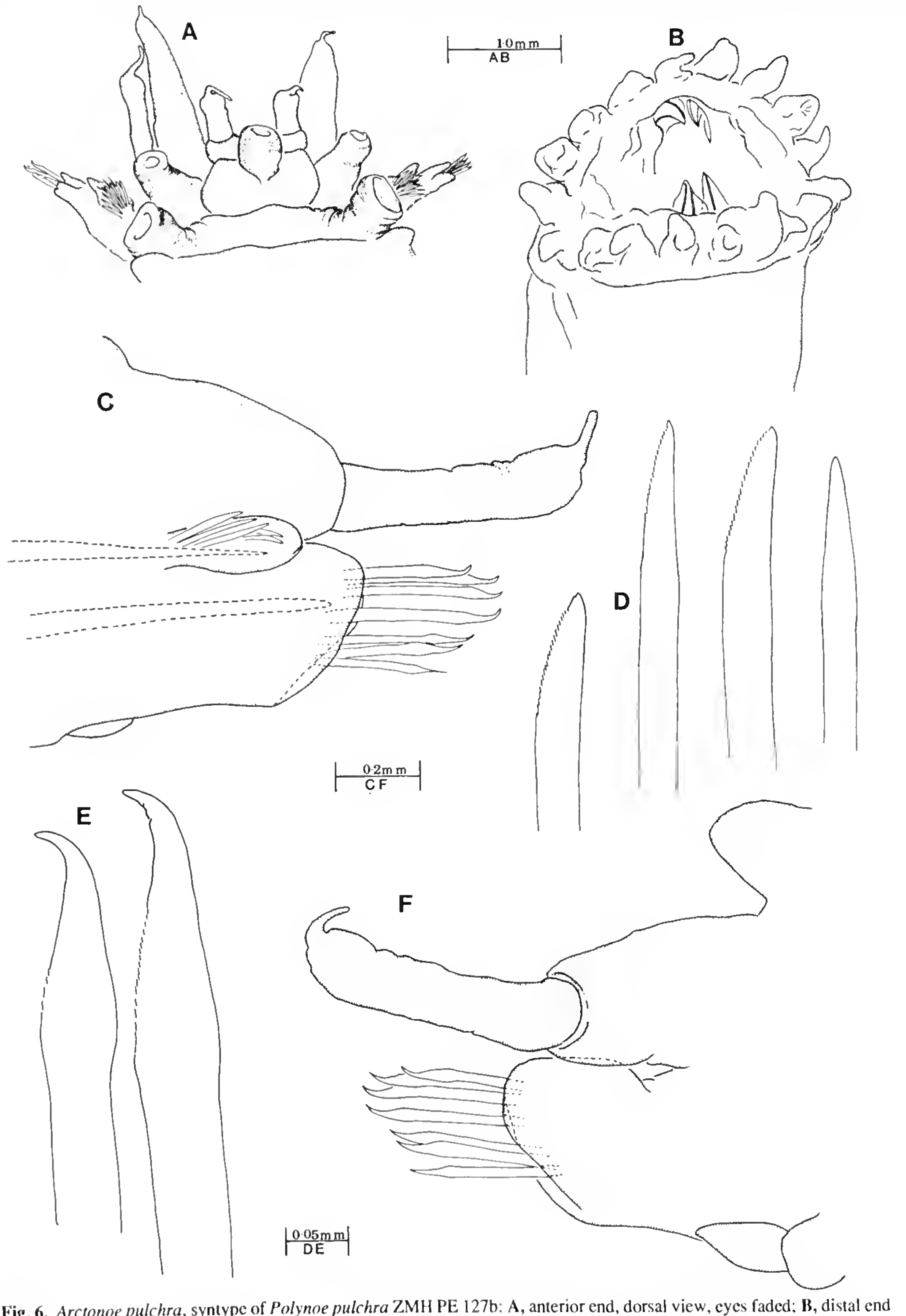

Fig. 6. *Arctonoe pulchra*, syntype of *Polynoe pulchra* ZMH PE 127b: **A**, anterior end, dorsal view, eyes faded; **B**, distal end of everted pharynx; **C**, anterior view of cirrigerous parapodium from segment 12; **D**, notosetae; **E**, neurosetae; **F**, posterior view of cirrigerous parapodium from segment 12.

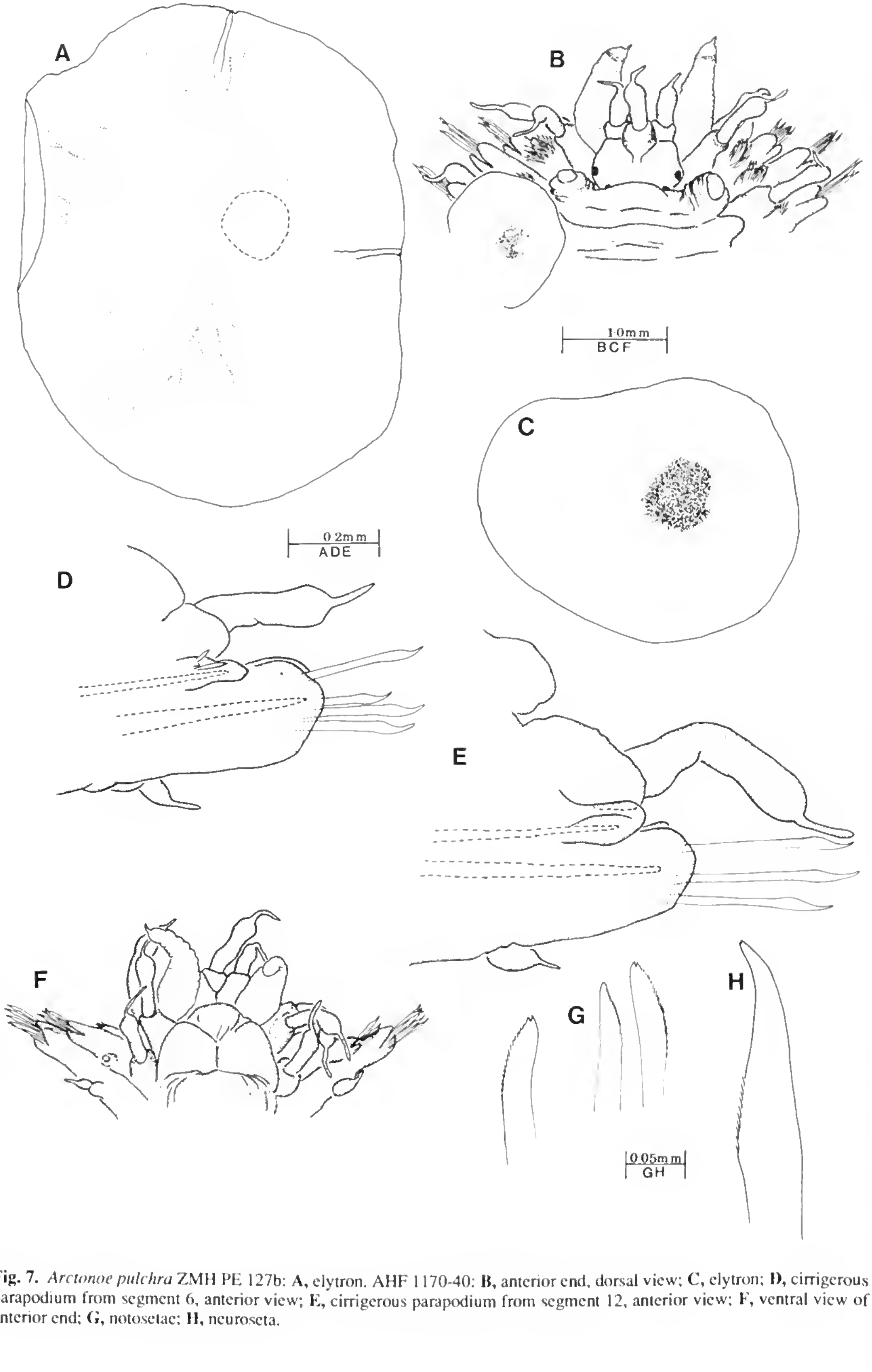

Fig. 7. *Arctonoe pulchra* ZMH PE 127b: **A**, elytron. AHF 1170-40: **B**, anterior end, dorsal view; **C**, elytron; **D**, cirrigerous parapodium from segment 6, anterior view; **E**, cirrigerous parapodium from segment 12, anterior view; **F**, ventral view of anterior end; **G**, notosetae; **H**, neuroseta.

Halosydna pulchra - Moore 1908:329-330; 1909:240; 1910:328-329; Treadwell 1914: 179; Berkeley 1923:212; 1924:193.

Acholoe pulchra - Hartman 1936:32.

Lepidasthenia pulchra - Treadwell 1937: 144-145.

Arctonoe pulchra - Hartman 1938:116; 1948:6; 1968:47; Banse and Hobson 1974:26; Berkeley and Berkeley 1941:24; 1942:188; 1948:21; Skogsberg 1942:497-500, Fig. D 6-8; Pettibone 1953:61-64, Pl. 30, Figs 272-280; Uschakov 1982:116.

Halosydna leioseta Chamberlin, 1919:2.

Halosydnoides vittata var. *pulchra* Seidler, 1924:136.

Type material. SYNTYPE - HZM PE 127b, label reads " Polynoe pulchra TYPEN-MATERIAL".

Additional material. AHF 1170-40, Southern California, Santa Catalina Island, 33°26' 45" – 33° 27' 10" N, 118° 27'10" – 118° 28'30" W, trawl, 80-100 fathoms, sponge gravel and sand, 10.viii. 1940, 13 specimens.

Description. Body dorsally flattened, widest about 1/3 from head, tapering rapidly anteriorly, gradually posteriorly. Length 10-26mm, width including parapodia 3-9.5mm. Variable number of segments (32-52), increasing with size. Dorsal and ventral surfaces of body without pigment.

Numerous pairs of large soft elytra attached on segments 2, 4, 5, 7, 9, alternate segments to 23, 26, 28, 29, 31, 33, thereafter on alternating segments to end of body. One specimen with asymmetrical arrangement of elytra after segment 39, with on the left side a pattern similar to the other specimens but on the right side the elytra were found on segments 39, 40, 41, 44, 46, 48, and 50. Elytra smooth, without tubercles or papillae, with smooth margins, slightly folded on some specimens (Fig. 7A,C). Elytra overlap posteriorly, and often medially, covering dorsum entirely on some specimens. Some specimens with a large central dark brown spot on elytra (Fig. 7C).

Prostomium bilobed, much wider than long, without cephalic peaks (Figs 6A, 7B). Two pairs of eyes, anterior pair moderate size, circular to oval, lying laterally at widest part of prostomium, posterior pair near posterior border, relatively close behind anterior pair and closer to midline. Palps short, stout, with abruptly tapered tips, and, on most specimens examined, some faint, irregular annuli (Fig. 7B). Median antenna with large, cylindrical ceratophore inserted in anterior notch, style smooth, basally cylindrical, expanding into subterminal inflation and a long filiform tip. Lateral antennae with distinct ceratophores shorter and thinner than median ceratophore, inserted terminoventrally on prostomium (Figs 6A, 7B), converging midventrally (Fig. 7F), antennae shorter than median antenna, basally cylindrical, expanding into slight subterminal inflation and long filiform tip.

Tentacular (first) segment not visible dorsally, achaetous (although one of the specimens had a seta on the base of the right tentaculophore), tentaculophores moderately long, lateral to prostomium, two pairs of tentacular cirri, smooth, similar length and shape, to median antenna. Facial tubercle poorly developed. Segment 2 without nuchal fold, with first pair of elytra, subbiramous parapodia, and ventral buccal cirri longer than following ventral cirri.

Parapodia subbiramous (Figs 6C,F, 7D,E). Notopodium small, digitiform, on anterodorsal face of much larger, neuropodium. Neuropodia deeply cut dorsally forming bluntly rounded presetal and postsetal lobes of similar length, presetal sometimes slightly longer, (Figs 6C,F, 7D,E). Cirrophores of dorsal cirri on segments without elytra, large cylindrical, styles thick, basally cylindrical expanding into weak subterminal inflation and short filiform tip. Dorsal tubercles conspicuous knobs. Ventral cirri short, subulate. Nephridial papillae well developed on larger specimens, beginning on segments 6-12, continuing to end of body, on smaller specimens papillae often inconspicuous. Notosetae (Figs 6D, 7G) short, slightly curved, with rows of serrations and tips blunt or notched. On small specimens notosetae present on all parapodia, decreasing in number posteriorly; on larger specimens notosetae present only on anterior segments. Neurosetae large, stout, present from segment 2 onwards, with prominent subdistal swelling, faint rows of serrations and strongly bent unidentate tips (Figs 6E, 7H).

Pygidium small, anus terminal, no evidence of anal cirri. Commensal with asteroids, holothurians, echinoids, molluscs and terebellid polychaetes.

Distribution. Northeast Pacific: Alaska to lower California.

Remarks. Johnson's (1897) description of this species was based on specimens collected from holothurians and keyhole limpets. All of the polychaete material described in his paper was deposited in the Museum of the University of California (Johnson 1897:155). Curiously, a request for material sent to a number of European Museums produced a specimen from the Hamburg Museum which is labeled as" Co-type *Polynoe pulchra*". At first, I considered the status of this specimen as doubtful as there is no mention by Johnson of an intention to deposit type specimens overseas. However, Dr Gesa Hartmann-Schröder (pers. comm.) has confirmed that the specimen was given to Ehlers either by Johnson or someone at the University of California Museum.

The description of the species given by Johnson is a good one, providing vital information on the number of elytra, the pattern of arrangement on the body and the species is well figured. The species is similar to *A. vittata* but can be distinguished from it primarily by the presence of only one kind of neuroseta. I have not been able to find on the specimens I have examined the 'short, close set papillae on dorsolateral body lobes, parapodia, and dorsal tubercles as described by Pettibone (1953). Nevertheless there is good general agreement with the original description.

Genus *Gastrolepidia* Schmarda 1861

Gastrolepidia Schmarda 1861:159 (type species *Gastrolepidia clavigera* Schmarda, 1861, by monotypy. Gender: feminine).

Diagnosis. Body flattened, elongate, segments up to 60. Elytra large, smooth, margins with pocket-like fold on inner margin, up to 31 pairs on prominent elytrophores on segments 2, 4, 5, 7, 9, alternate segments to 23, 26, 29, 32, 35, 36, and thereafter usually on alternating segments to end of body but sometimes with considerable variation including asymmetry. Conspicuous ventral lamellae at the base of each parapodium from segment 3 onwards. Prostomium bilobed, much wider than long, without cephalic peaks, with three clavate antennae. Median antenna ceratophore large, inserted in anterior notch, Lateral antennae with distinct ceratophores inserted terminoventrally on prostomium, converging midventrally on the underside of the prostomium. Two palps, short, slender tapering gradually to fine tips. Two pairs of eyes, on posterior half of prostomium. First or tentacular segment not visible dorsally, facial tubercle a well developed knob, tentaculophores lateral to the prostomium, achaetous, with two pairs of dorsal and ventral tentacular cirri, smooth. Second or buccal segment with conspicuous semilunar nuchal fold, with first pair of elytra on prominent elytrophores, subbiramous parapodia and ventral buccal cirri much longer than following ventral cirri. Pharynx large, muscular, distally eleven pairs of soft papillae encircling mouth with two pairs of chitinous jaws. Parapodia subbiramous, notopodia small, with long spatulate acicular lobe, neuropodia larger, deeply incised dorsally and ventrally forming well developed presetal and postsetal lobes. Notosetae short to long, curved, with rows of serrations along the outer edge, and notched tips. Neurosetae longer, of two kinds: upper ones slender, with many rows of serrations and hooded, notched tips; middle and lower ones much stouter with fewer rows of serrations and slightly curved, unidentate tips. Dorsal cirri with cylindrical cirrophores and clavate styles. Dorsal tubercles indistinct. Ventral cirri short, smooth, tapering gradually to filiform tips. Nephridial papillae usually well developed, beginning on segments 6-8, continuing to end of body. Anus terminal, a pair of anal cirri on short cirrophores, styles very similar to styles of antennae and dorsal cirri.

Distribution. Tropical Indo-West Pacific.

Remarks. *Gastrolepidia* is similar to *Arctonoe* in prostomial features, such as eye position, insertion of lateral antennae, lack of cephalic peaks, and shape of antennae. The body is elongate with a variable number of soft flexible elytra, as in species of *Arctonoe*. The neuropodia are similarly deeply cut dorsally and ventrally, forming distinct anterior and posterior lobes and the notopodium is small. The middle and lower neurosetae resemble those of *Arctonoe*, and the notosetae show some similarities. For these reasons *Gastrolepidia* is also placed in the new subfamily Arctonoinae. Major differences between *Gastrolepidia* and *Arctonoe* are the

pattern of elytron attachment, the presence of ventral lamellae on *Gastrolepidia*, and the long, fine, hooded upper neurosetae of *Gastrolepidia*.

Gastrolepidia clavigera Schmarda
(Figs 8A-H, 9A-F, 10A-G)

Gastrolepidia clavigera Schmarda, 1861: 159, Pl. XXXVI, Fig. 316; Baird 1865: 173; Quatrefages 1865:287, 288; Grube 1876:69; Willey 1905:253; Potts 1910:341; Horst 1915a:11, 12; 1917:84, Pl. XVI, Fig. 5; Fauvel 1919:335; 1930:13, Pl. 1, Figs 16-19; 1932:25; 1940:254; 1947:19, Fig. 15a-d; 1953:51, Fig. 22d-f; Seidler 1924:142, Figs 19-20; Augener 1926:443, Fig. 2; 1927:361; Monro 1931:7; Hartman 1954:630, Figs 174B-E; Day 1967:51, Figs 1, 5a-f; Reish 1968:210; Gibbs 1969:447-449, Fig. 130; 1971:119; 1972:203; Uschakov 1982:118-120, Pl. XXXVII, Figs 8-12, Pl. XXXVIII, Figs 5, 6; Devaney and Bailey-Brock 1987:97, 98.

Gastrolepidia amblyphyllus Grube, 1876: 69; 1878:46, Pl. III, Fig. 7.

Polynoe freudenbergi Plate, 1916:18-21, Pl. 9, Figs 1, 2, Textfigs A-C.

Type material. SYNTYPES - NMW Inv. No. 296, Ceylon, coll. Musei Vindobonensis, 18??, 3 specimens, one complete in 3 pieces, and 2 anterior ends.

Additional material. MNHN No. 1923, Madagascar, Tamatave, 4.ii.1912, coral reef, W. Kaudern. MNHN A339, Indian Ocean (Mus.Calcutta), station 669, collection P. Fauvel, AHF N5932, Bikini Atoll. ZMA V. Pol. 320, Siboga station 60, Hiangsisi, Samau Island, Reef, from *Holothuria atra*, Siboga station 213, Palu Pasfi, Tanette litt. 2 specimens. NTM W3950, 3951, Singaraja, Bali, 13.iv.1984, coral reef, on *Bohadschia argus*, 2m, coll. C. Watson-Russell. AM W5133, Between Bird and South Islands, 27.xi.1985, Reef floor, from underside of *Bohadschia argus*, 10m, coll. Hutchings and Reid. AM W5144, same locality and collectors, from *Stichopus variegatus*, ?.xi.1985, 2 specimens. AM W5498, same locality, host and collectors, 24.xi.1985, 15m, 2 specimens. AM W5143, Granite Bluff, Lizard Island, 30.xi.1985, from underside of *Bohadschia argus*, 20m, coll. Hutchings and Reid.

ASHMORE REEF, NORTHWESTERN AUSTRALIA, 12° 14'S 122° 58'E: NTM W3952, on *Bohadschia argus*, 29.vii.1986, intertidal, coll. C. Johnson; NTM W4189, Coral rubble and sand, from holothurian, 27.vii.1986, 1m, coll. H. Larson; NTM W4998, on *Stichopus hermeni*, 24.ix.1987, low water, coll. A. Hoggett; NTM W4930, 4681, 4540, from *Bohadschia argus*, coral outcrop, 3-10m, 11.iv.1987, coll. R. Hanley, L. Vail; NTM W4447, on *Holothuria atra*, low water, 14.iv.1987, coll. R. Hanley; NTM W4420-4422, 4424, from *Holothuria atra*, reef flat, low water spring, 14.iv.1987, coll. R. Hanley; NTM W4724, on *Bohadschia argus*, Coral bommie, 18m, 19.iv.1987, coll. L. Vail; NTM W4728, 4532, on *Bohadschia argus*, lagoon, 2-10m, 20.iv.1987, coll. R. Hanley; NTM W4438, from *Holothuria atra*, reef flat, low water, 21.iv.1987, coll. R. Hanley; NTM W4431-4434, 4437, on *Bohadschia argus*, Reef flat, low water, 22.iv.1987, coll. R. Hanley.

HERON ISLAND, QUEENSLAND, coll. N. Coleman: AM W5626, Wistari Reef, on large green holothurian with black spots, 24.vii.1973; AM W6859, 10m, 25.xi.1971; AM W6890, from *Stichopus variegatus*, ?/12/ 1974; AM W8678, on holothurian, 8m, 23.vii.1975; AM W9166, on holothurian, 10m, 5.viii.1976. AM W5449, Warroora, northwestern Australia, on holothurian, 4ft, 19.vii.1972, coll. N. Coleman. AM W6014, 6015, John Brewer Reef, Queensland, on holothurians, 5m, 14.ii.1974, coll. N. Coleman. AMPI Worm No. 294, Lizard Island, Queensland, on holothurian, lagoon, 5m, 13.i.1979. Australian Museum, North Point, Lizard Island, found on *Bohadschia argus*, March, 1986, coll. Reid and Hutchings.

Description. Body flattened, widest part of body in anterior third, tapering anteriorly and posteriorly, with up to 63 segments.

Pigmentation of specimens extremely variable, depending on coloration of host (see Potts 1910; Gibbs 1969).

Elytra large, soft, smooth without papillae on margins (Figs 9C, 10A,B). Variable number of pairs of elytra (15-31) attached on segments 2, 4, 5, 7, 9, alternate segments to 23, 26, 29, 32, 35, and 36, thereafter attachment pattern varying between specimens, usually on alternating segments to end of body but some specimens with elytra on consecutive segments and/or asymmetrical (Table 3). Elytra overlapping medially and posteriorly (Fig. 9C). Elytron with pouch on

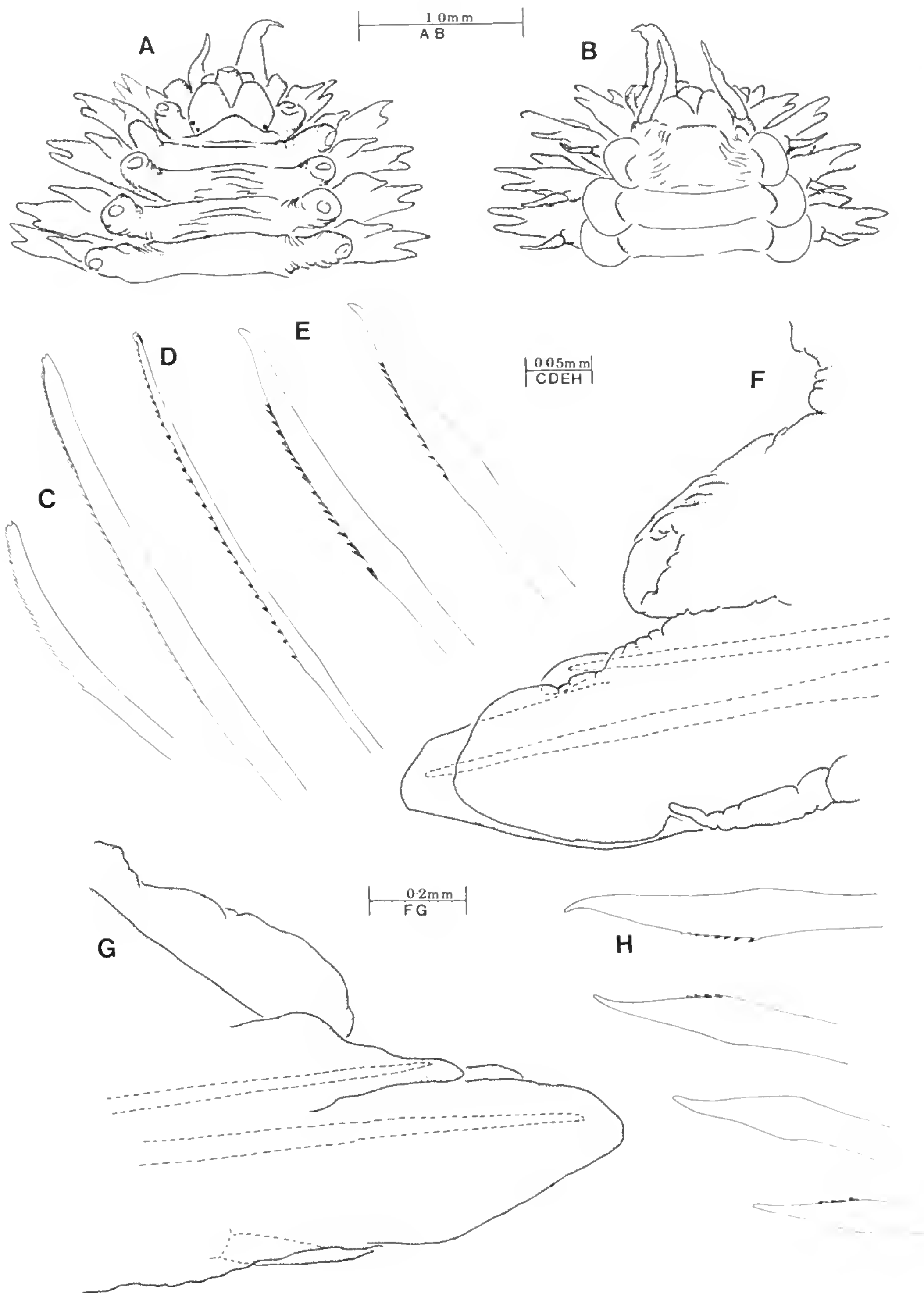

Fig. 8. *Gastrolepidia clavigera* syntype: **A**, anterior end, dorsal view; **B**, ventral view of anterior end; **C**, notosetae; **D**, upper neuroseta; **E**, middle neurosetae; **F**, posterior view of cirrigerous parapodium, style of dorsal cirrus missing ; **G**, anterior view of same; **H**, middle and lower neurosetae.

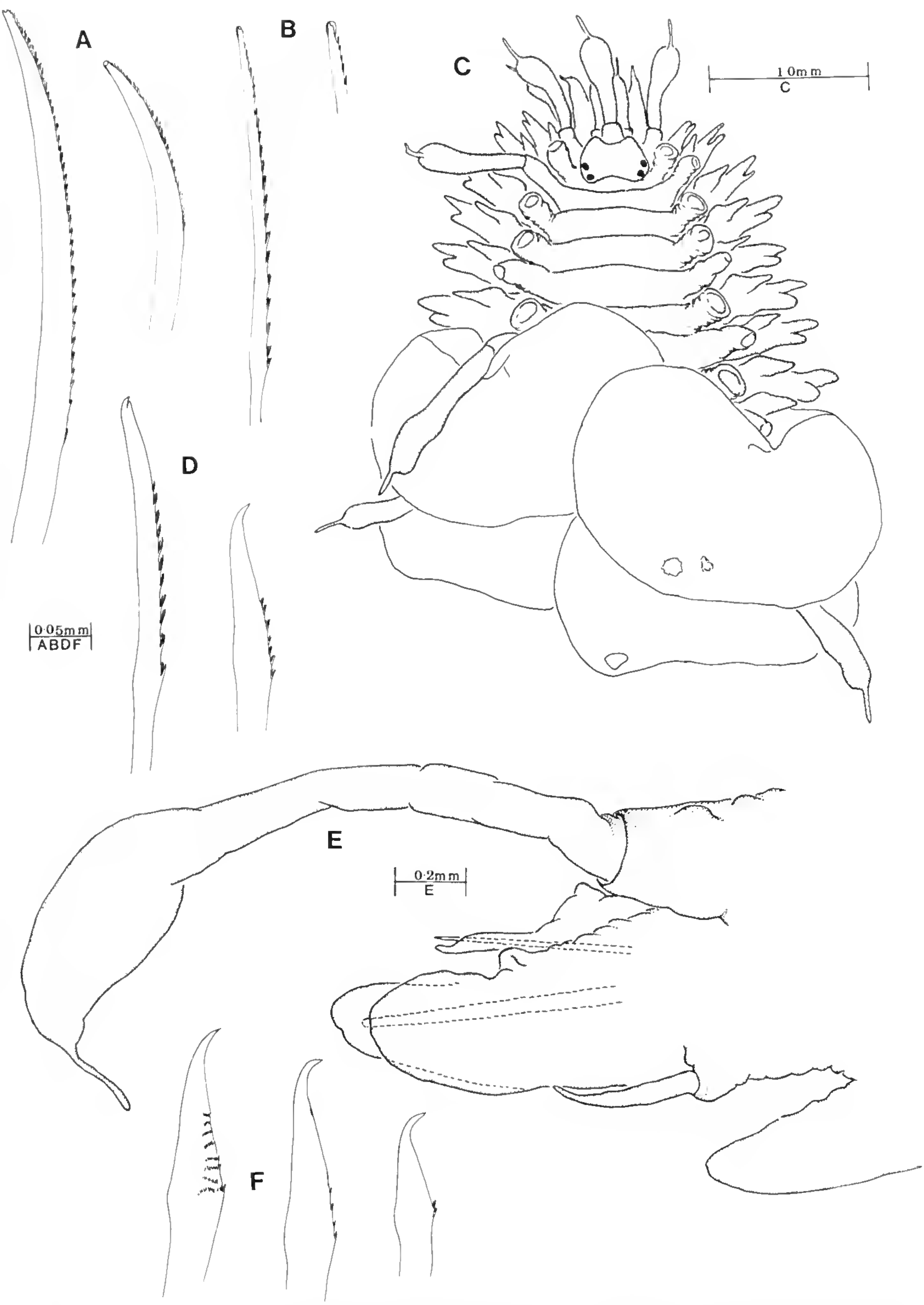

Fig. 9. *Gastrolepidia clavigera* MNHN A339, **A,B,D-F**; NTM W4420, **C**,: **A**, notosetae; **B**, upper neuroseta; **C**, dorsal view of anterior end showing orientation of dorsal cirri and elytra; **D**, middle neurosetae; **E**, cirrigerous parapodium, posterior view; **F**, middle and lower neurosetae.

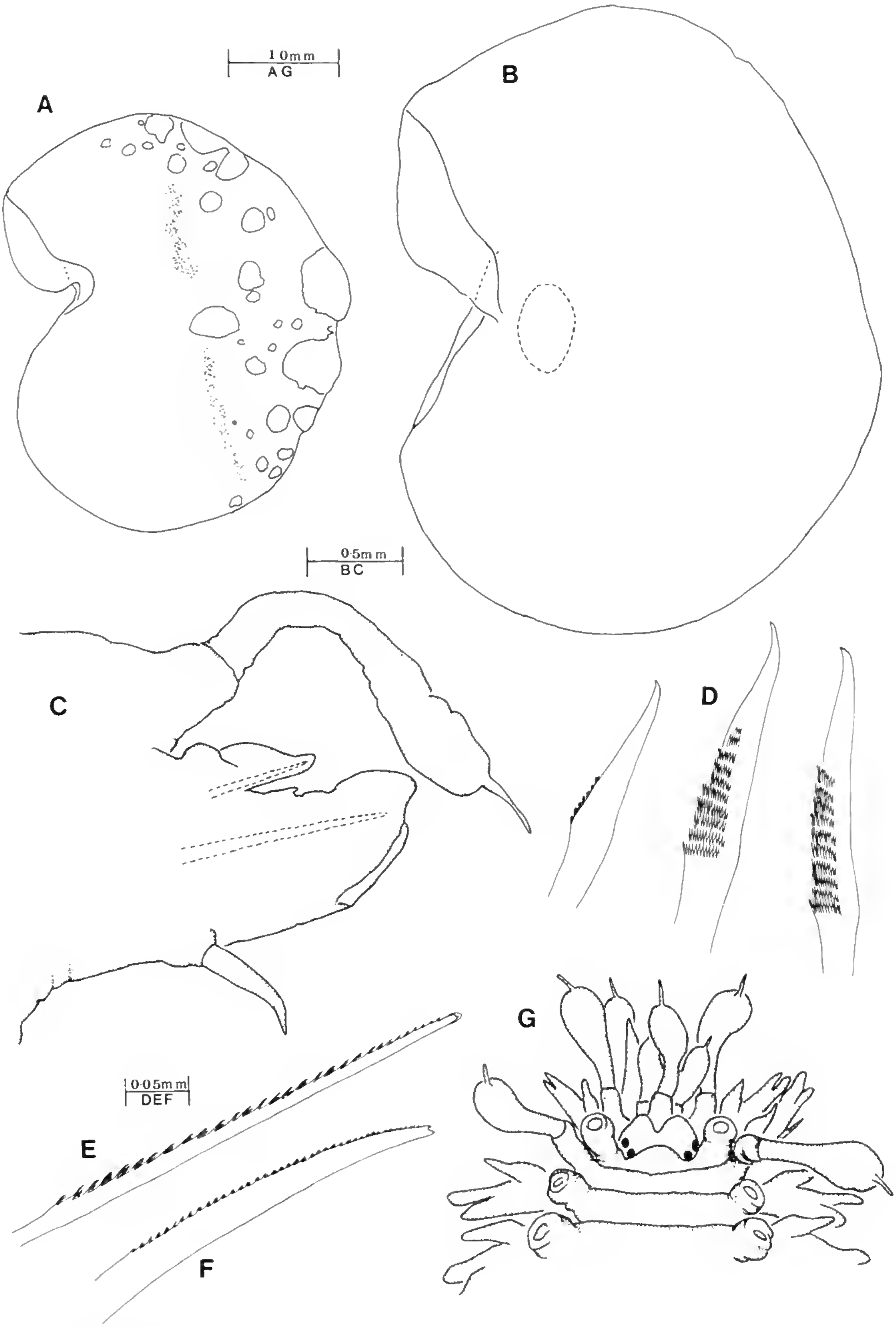

Fig. 10. *Gastrolepidia clavigera* NTM W4424: **A**, posterior elytron. MNHN A339: **B**, posterior elytron. AM 5144: **C**, cirrigerous parapodium; **D**, lower and middle neurosetae; **E**, upper neurosetae; **F**, notoseta. NTM W4424: **G**, anterior end, dorsal view.

Table 3. Variation of elytron attachment pattern on specimens of *Gastrolepidia clavigera* with 19 or more pairs of elytra

Specimen	*Length*	*Width*	*No. of segments*	*No. of pairs of elytra*	*Elytra attached on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32*
AM W5144 (A)	20mm	6.3mm	42	19	35, 36, 39, 40
AM W5144 (B)	16mm	5mm	47	21	35, 36, 38, 39, 41, 45
NTM W3952	18.6mm	6mm	53	26	35, 36, 38, 40, 42, 44, 46, 47, 48, 50, 51
NTM W4189	18mm	7mm	49	22+2odd ones	35, 36, 38, 39 (left), 41, 42, (right), 43, 45, 47
ZMA Siboga Expd. Palu Pasfi	25mm	7mm	41	19	35, 36, 38, 40
ZMA V. Pol 320	21mm	6.5mm	48	23	35, 36, 38, 39, 42, 44, 46, 48
MNHN # 1923	20mm	5mm	51	21	35, 38, 41, 44, 45, 48
NTM W4422	13mm	3.5mm	45	21	35, 36, 38, 40, 42, 44
NTM W4998	29mm	7.5mm	63	31	35, 36, 38, 40, 42, 44, 46, 48, 50, 51, 53, 55, 57, 59, 61 left side 35, 36, 38, 40, 42, 44, 46, 48, 50, 52, 53, 55, 57, 61, 63 right side.
NTM W4540	18mm	5.2mm	50	23	35, 36, 39, 41, 43, 45, 47, 49
NTM W5449	17mm	5mm	50	23	35, 36, 38, 40, 42, 45, 47, 49
AM W6014	17mm	6.5mm	40	19	35, 36, 38, 40
AM W6015	13.5mm	4mm	42	19	35, 36, 38, 40 left 39, 41 right
AM W6859	15mm	5mm	47	23	35, 36, 38, 39, 41, 42, 44, 45
NTM W4434	11mm	4mm	41	19	35, 36, 38, 40
NTM W4432	18mm	4mm	51	24	35, 36, 38, 40, 42, 44, 46, 49, 51
NTM W4532	18mm	5.4mm	42	21	35, 36, 38, 39, 41, 42

anterior margin with margin folded over surface (Figs 9C, 10A,B), and a small area of overlap on anterior side of the elytrophore scar, with margin overlapping (Fig. 10B); small indentation in the margin created by the folded pouch usually occupied by cirrophore of dorsal cirrus of preceding segment (Fig. 9C).

Prostomium bilobed, much wider than long, without cephalic peaks (Figs 8A, 9C, 10G). Two pairs of eyes, anterior pair large, lying dorsolaterally at widest point of prostomium, posterior pair slightly smaller (sometimes larger), lying close behind anterior pair and closer to midline. Palps, short, tapering gradually to a filiform tip. Ceratophore of median antenna large, truncated, inserted in anterior notch, with style smooth, basally cylindrical and expanding into large bulbous subterminal inflation, then abruptly tapering to filiform tip. Ceratophores of lateral antennae distinct, much shorter and smaller than median, inserted terminoventrally on distal ends of prostomium (Figs 8A,B, 10G), converging midventrally on underside of prostomium; styles similar to median antenna but usually shorter.

Tentacular (first) segment, not visible dorsally, tentaculophores lateral to prostomium, achaetous, with two pairs of dorsal and ventral tentacular cirri, smooth, similar in length and shape to median antenna. Facial tubercle well developed knob. Segment 2 with semilunar nuchal fold (Figs 8A, 9C, 10G), first pair of large elytrophores, subbiramous parapodia, and ventral buccal cirri longer than following ventral cirri.

Parapodia subbiramous (Figs 8F,G, 9E, 10C). Notopodium small, subconical with long flattened acicular lobe (Figs 8G, 9E, 10C). Neuropodium deeply cut dorsally and ventrally forming longer, thinner, sharply rounded presetal lobe and shorter, bluntly rounded postsetal lobe (Figs 8F,G, 9E, 10C). Dorsal cirri on segments without elytra, with cylindrical cirrophores and long, smooth styles, basally cylindrical, expanding into large subterminal inflation and abruptly tapered filiform tip (Figs 9E, 10C). Ventral cirri short, on small cirrophores, styles tapering gradually to a filiform tip. Nephridial papillae not visible on some specimens, usually beginning on segments 6-8, and continuing to end of body. Ventral lamellae large, conspicuous, on the bases of parapodia from segment 3 onwards (Fig. 8B, 9E).

Notosetae (Figs 8C, 9A, 10F) short to long, curved, with rows of serrations along outer edge, with notched tips. Neurosetae long, straight; upper group slender with numerous

rows of serrations and hooded, notched tips (Figs 8D, 9B, 10E); middle group stout, with fewer rows of serrations and slightly curved, unidentate tips (Figs 8E,H, 9D,F, 10D); and lower group similar with very few rows of serrations (Figs 8H, 9F, 10D).

Pygidium small, anus terminal, with pair of anal cirri resembling dorsal cirri.

Commensal on holothurians.

Distribution. Tropical Indo-West Pacific.

Remarks. The type material includes 3 syntypes, one complete, although fragmented, and two anterior ends. The complete syntype is the smallest, measuring 12mm in length, 3.5mm in width including parapodia, with 40 segments and 17 pairs of elytrophores (elytra all missing); no eyes are present, presumably they have faded during the specimens' long storage in alcohol. Styles of antennae, tentacular, dorsal and anal cirri all missing. However, the features of ventral lamellae, elytral arrangement, parapodia and setae are consistent with those described by Schmarda and subsequent authors.

The other two syntypes are incomplete. One an anterior fragment with prostomium (no eyes) and 14 segments, without elytra. The other specimen also has 14 segments, prostomium with posterior pair of eyes present and several elytra still attached. Both of these syntypes agree well with the description of the species I have given above.

In the original description Schmarda emphasised the unusual ventral lamellae (hence the generic name), and indicated that he thought they were similar in structure to the elytra, but provided little information on the rest of the animal. My examination of the ventral lamellae shows that the resemblance between these two structures is entirely superficial. The ventral lamellae are outgrowths of the body, whereas the elytra are highly modified dorsal cirri.

Grube (1876), briefly described another species, *Gastrolepidia amblyphyllus*, based on material from the Philippines, and in 1878 he provided another, more comprehensive description. Grube erected the new species because the ventral lamellae on the specimens he examined were not like elytra, as Schmarda had claimed in his description of *G. clavigera*. In both papers, Grube recognised that his new species might just be a variety of *G. clavigera*, as he was uncertain of Schmarda's interpretation of the ventral lamellae and had not seen the type material of *G. clavigera*.

Willey (1905) appears to have been the first author to synonymise *G. amblyphyllus* with *G. clavigera*, and this has been followed by all subsequent authors.

Willey (1905) and Potts (1910) indicate that the pattern of elytron attachment is invariable on all specimens examined. In their view the elytra were attached on 2, 4, 5, 7, etc. to 23, 26, 29, 32, 35, 36, 38, 39, and on alternate segments to the end of the body. Horst (1917) disagreed with this view, noting that on the specimens he examined there was some variation in attachment pattern after segment 36.

Subsequent descriptions (Augener 1926; Fauvel 1932, 1947; Day 1967; Uschakov 1982) added little additional information. Hartman (1954), was the first to record that the ventral lamellae begin on segment 3 and that the notosetae are capped by a delicate, hyaline hood; she did not mention the presence of similar hoods on the slender upper neurosetae.

Potts (1910) was the first to recognise that the association between *G. clavigera* and different holothurian hosts was the reason for the different color patterns observed on specimens of *G. clavigera*. Gibbs (1969, 1972) provides a list of the different holothurian hosts and suggests that the ventral lamellae might be an adaptation to life on a holothurian, allowing the worms to cling by suction to their hosts. Uschakov (1982) suggests that the ventral lamellae might have a reproductive function, and may only be present on large specimens. He records a small specimen of this species which did not have ventral lamellae. However, I consider this record as dubious, as specimens examined in my study ranged from 11mm to 29mm and all had well developed ventral lamellae beginning on segment 3. It is also interesting to note that the large specimen described by Uschakov (1982) was collected from *Pinna* overgrowth, whereas most of the records of this species indicate it is found on holothurians. Although many of the early records do not indicate hosts this is probably because the material was collected by dredge or trawl, in which case commensals are often separated from their hosts.

Incidentally, although no previous record emphasises that the ventral lamellae begin on

segment 3, this feature is one easy way to distinguish members of this genus from members of the genus *Paralepidonotus* Horst, 1915a, in which the very similar, though smaller ventral lamellae always begin on segment 4.

Genus *Bathynoe* Ditlevsen

Weberia Horst, 1915b:246 (type species *Weberia pustulata* Horst, 1915b, by monotypy; preoccupied in 1830 by *Weberia* Robineau-Desvoidy (Diptera)).

Bathynoe Ditlevsen, 1917:42 (replacement name; cf. Pettibone and Augener 1970:205. Gender: feminine).

Bathynoe tuberculata (Treadwell)
(Figs 11A-F, 12A-D)

Harmothoe tuberculata Treadwell, 1906: 1154

Arctonoe tuberculata - Hartman 1938:117, Fig. 37,e,f; 1956:260, 265; 1966:174; Uschakov, 1982:116.

Type material. HOLOTYPE - USNM 5205, Hawaii, vicinity of Niihau Island, commensal in actinostome of *Brisinga*, station 4177, on bottom of fine gray sand, 451-319 fms, coll. U.S. Fish Commission steamer *Albatross*.

Description. *Holotype*: Body short, flattened, tapering gradually anteriorly and posteriorly. Length 14.5mm, width including parapodia 4.6mm. Thirty five segments. From second segment onwards, dorsum with conspicuous digitiform tubercles medially, one on each segment (Fig. 11A). Entire body grey.

Elytra all missing, prominent elytrophores 18 pairs on segments 2, 4, 5, 7, alternate segments to 24, 26, 27, 29, 30, and 32.

Prostomium bilobed, wider than long, without cephalic peaks (Fig. 11A). Right side of prostomium damaged. Eyes absent. Two palps, both distorted and incomplete distally. Three antennae, all styles missing. Median ceratophore large, cylindrical, inserted in anterior notch. Lateral ceratophores larger than median ceratophore, inserted terminoventrally on the distal ends of the prostomium, converging in the midline on the underside of the prostomium (Fig. 11B).

Tentacular (first) segment, not visible dorsally, tentaculophores lateral to prostomium, achaetous, long, stout, with two pairs of tentacular cirri, only right ventral tentacular cirrus remaining, smooth, basally cylindrical, expanding into pronounced subterminal inflation and abruptly tapered to short filiform tip. Facial tubercle weakly developed. Segment 2 with large medial digitiform tubercle (Fig. 11A), first pair of elytrophores (elytra missing), subbiramous parapodia, and ventral buccal cirri (one on right side missing, Fig. 11B). Neuropodium of second segment with presetal lobe bluntly rounded, postsetal lobe shorter, straight. Base of postsetal lobe with long, digitiform lobe attached ventrally and deflected upwards, ending distally in two papillae-like projections.

Parapodia subbiramous (Figs 11C, 12A, C). Notopodium similar length to neuropodium, with long, digitiform acicular lobe,deflected upwards, slightly inflated distally. Neuropodium deeply cut dorsally, with longer, bluntly rounded presetal lobe (Fig. 12C), postsetal lobe shorter, bluntly rounded (almost straight), with digitiform lobe attached basally and deflected upwards (Figs 11C, 12A), outer edge and tip with densely packed papillae (= branchia, Treadwell, 1906). Cirrophores of dorsal cirri on segments without elytra, large, cylindrical, basally joined to conical, well-formed dorsal tubercles by fleshy ridge. Styles of dorsal cirri all missing (Fig. 12A). Ventral cirri absent from segment 3 onwards (Fig. 11D). Nephridial papillae not found.

Notosetae absent. Neurosetae, 5-10 on each parapodium, large, stout, straight, with subdistal swelling and several rows of very faint serrations between swelling and strongly curved unidentate tip (Figs 11E, F, 12B, D). Many tips of neurosetae broken or split.

Nephridial papillae not found.

Pygidium small, anus appears to be terminal, condition of specimen poor posteriorly, not possible to determine whether anal cirri were present.

Holotype ovigerous.

Commensal on asteroid of genus *Brisinga*.

Distribution. Known only from the type locality in the Hawaiian Islands, in 451-319 fathoms.

Remarks. The original description differs from the one given here in a few important respects. Treadwell (1906) states that there are 13 pairs of elytrophores, whereas I have

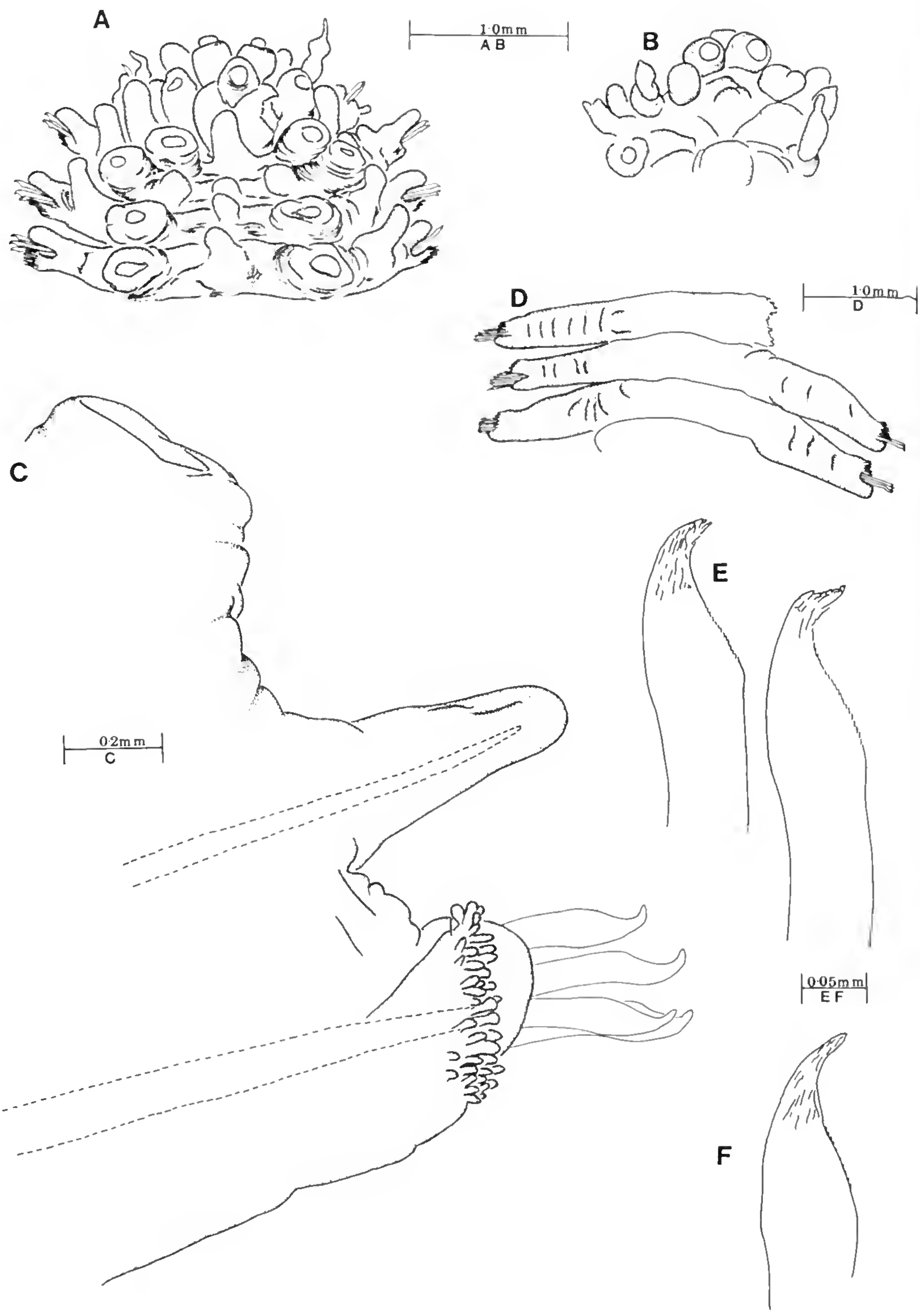

Fig. 11. *Bathynoe tuberculata*, holotype of *Harmothoe tuberculata* USNM 5205: **A,** anterior end, dorsal view; **B,** ventral view of anterior end; **C,** posterior view of elytragerous parapodium; **D,** ventral view of segments from middle of the body, note absence of ventral cirri; **E,F,** neurosetae, tips cracked and split.

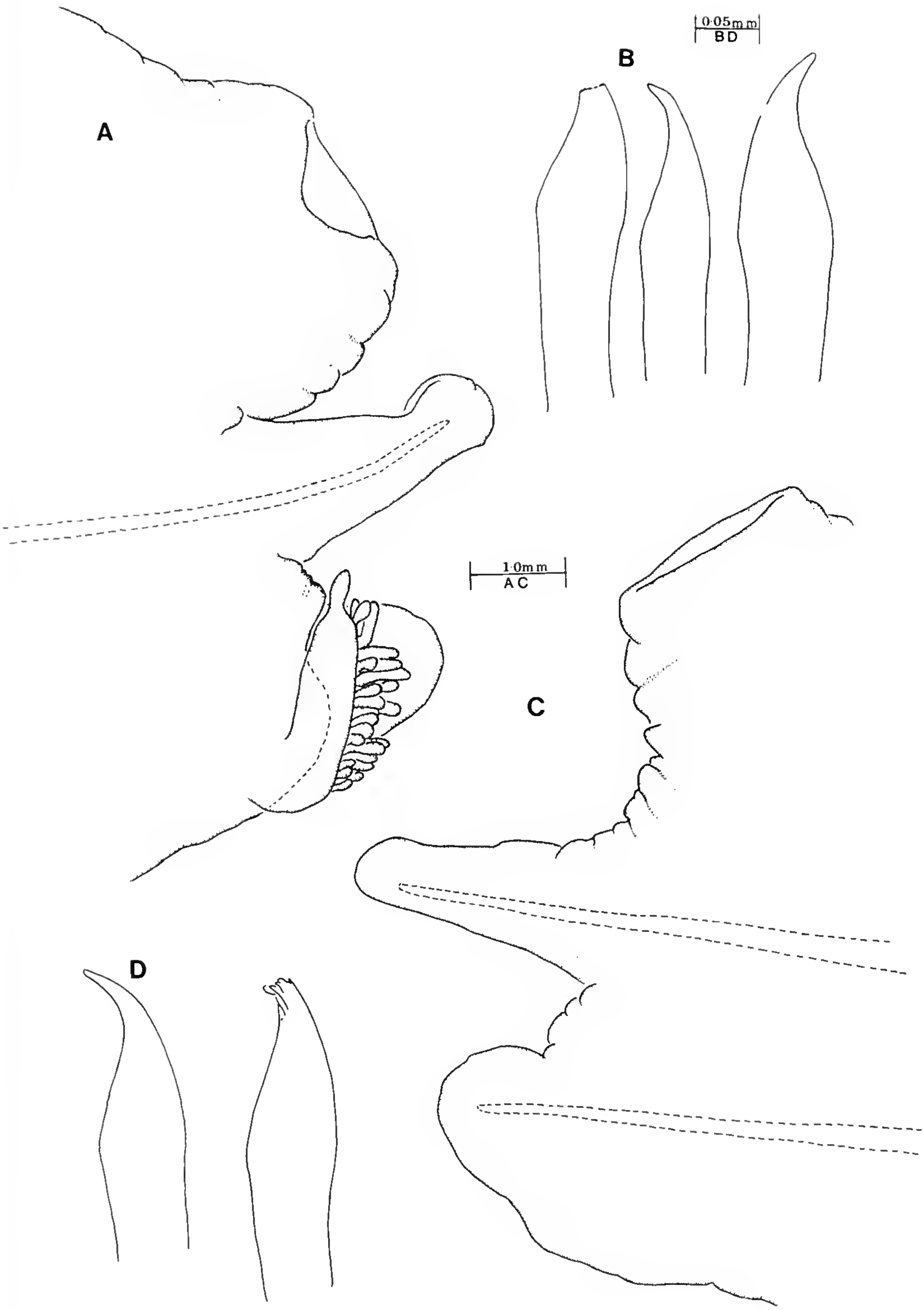

Fig. 12. *Bathynoe tuberculata* holotype: **A**, anterior view of cirrigerous parapodium; **B**, neurosetae; **C**, posterior view of elytragerous parapodium; **D**, neurosetae.

recorded 18. The poor condition of the specimen posteriorly, coupled with the close similarity in shape and position of cirrophores and elytrophores probably misled Treadwell. Indeed, I may have misinterpreted the structures on the last three segments of the body so that there may be more than 18 pairs of elytrophores. However, I believe there are dorsal tubercles present on these last few segments and therefore they are all cirrigerous.

Treadwell records the arrangement of elytrophores on the body as attached to segments 1, 2, 5, 7, etc., which I found to be incorrect in several respects.

According to Treadwell, segments 3 and 4, have dorsal cirrophores, which is incorrect as nowhere on the body, except for the last three segments, are elytragerous segments ever separated by more than one cirrigerous segment. The pattern of arrangement given by Treadwell implies that after the first few segments, the elytragerous and cirrigerous segments alternate until the end of the body, which is incorrect as there are adjacent elytrophores on segments 23 and 24, 26 and 27, 29 and 30.

The peculiar digitiform lobe on the postsetal side of each neuropodium has large papillae-like projections, which Treadwell (1906) called branchiae. I have found no evidence to suggest a respiratory function for these structures. They are clavate, and similar to the sensory papillae found on the cirrostyles of many polynoid scaleworms. This similarity of papillae, and the digitiform appearance of the lobe led me to suspect it may have been the ventral cirrus, and initially I thought the ventral cirri were present but attached distally. However a re-examination of the specimen, and in particular the second segment which has a pair of ventral buccal cirri, revealed the unusual lobe is also present on this segment, and therefore the ventral cirri are indeed missing from subsequent segments.

Treadwell referred the species to *Harmothoe* Kinberg, 1856, but the diagnosis of this genus notes that species have 15 pairs of elytra, whereas Treadwell recorded only 13 pairs for his new species. The absence of notosetae is another character which would preclude it from *Harmothoe*.

Hartman (1938) referred the species to *Arctonoe*, primarily because of its large, falcate neurosetae. Her description is short, and does not mention the number of pairs of elytra that the specimen might have had, although in the emended generic diagnosis of *Arctonoe*, Hartman states "Elytra 18 pairs or more...".

Bathynoe tuberculata cannot be included in *Arctonoe* because the arrangement of elytra on the body is very different from that seen in the other three species currently placed in that genus (see above). Each of these species share the same pattern of attachment up to segment 33, i.e. 2, 4, 5, 7, alternate segments to 23, 26, 28, 29 and 31.

The original description of *Weberia pustulata* by Horst (1915b) describes the same pattern of elytron arrangement as that seen on the holotype of *B. tuberculata*. In many respects the description of *Weberia pustulata* agrees with that of *B. tuberculata*: both have 18 pairs of elytra, the same attachment pattern, similar digitiform, papillate lobes on the posterior lobe of the neuropodia, and the large tubercles on the dorsum. The two species may eventually prove to be synonyms, but a decision cannot be made until the types of Horst's species have been examined.

Ruff (1989) has recently described another species of *Bathynoe* from the northeast Pacific and also refers *Harmothoe tuberculata* Treadwell to *Bathynoe* for the first time. His assignment is followed here.

Genus *Asterophilia* gen. nov.

Type species *Asterophilia carlae* sp. nov. Gender: feminine.

Diagnosis. Body flattened, fusiform, fragile, up to 35 segments. Body without pigment. Elytra 15 pairs, on prominent elytrophores, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, and 32. Elytra large, soft, transparent. Prostomium bilobed, wider than long, without cephalic peaks. Two pairs of eyes on posterior half of prostomium, two palps, three antennae. Ceratophore of median antenna inserted in anterior notch, ceratophores of lateral antennae inserted terminoventrally on distal ends of prostomium, converging in midline on underside of prostomium. First or tentacular segment not visible dorsally; tentaculophores lateral to the prostomium, achaetous, with two pairs of dorsal and ventral tentacular cirri; facial tubercle absent. Second or buccal segment with small nuchal fold, first pair of elytra on prominent elytrophores, subbiramous parapodia, and ventral buccal cirri longer than following

ventral cirri. Parapodia subbiramous, notopodium small, on anterodorsal side of neuropodium, subconical with long, thin acicular lobe; neuropodium larger, deeply cut dorsally and ventrally, with longer presetal and shorter postsetal lobes, both bluntly rounded. Notosetae short to long, curved with rows of serrations and notched tips. Neurosetae long, upper ones slender with subterminal swelling, rows of serrations and hooded, notched tips; middle and lower ones much stouter, with subterminal swelling and fewer rows of serrations, middle ones with bi- or unidentate tips, lower ones with few rows of serrations and curved unidentate tips. Dorsal cirri present on segments without elytra, cirrophores large, cylindrical, styles smooth, cylindrical basally with subdistal inflation and filiform tip; dorsal tubercles absent. Ventral cirri short, tapered. Nephridial papillae present from about segment 6 onward. Anus terminal with anal cirri?

Commensal on asteroids.

Etymology. The generic name refers to the relationship between the polynoid and its asteroid host, from the greek *aster* (star) and *phile* (love).

Remarks. Reference to Fauchald (1977) demonstrates that there are a large number of polynoid scaleworm genera with 15 pairs of elytra. Many of them are monotypic. The creation of yet another monotypic genus of polynoid scaleworm with 15 pairs of elytra attached on segments 2, 4, 5, 7, alternate segments to 23, 26, 29 and 32, i.e. the most common arrangement, may not be universally accepted, but it is not presently possible to satisfactorily reconcile this species with any of the existing genera. *Asterophilia carlae* sp. nov. has prostomial features which ally it closely with *Gastrolepidia clavigera*, its parapodia and setae are also very similar morphologically to those of *G.clavigera*, as evidenced by Horst's (1917) incorrect identification of the two Siboga specimens as *G. clavigera*. These similarities with *G. clavigera* make *A. carlae* incompatible with most of the existing genera (mainly Harmothoinae) which have 15 pairs of elytra and the same attachment pattern. The only other genus which has the same number of pairs of elytra, the same attachment pattern, and also has terminoventral insertion of the lateral antennae on the prostomium is *Paralepidonotus* Horst, 1915a, and as *A. carlae* does not have ventral lamellae it cannot be aligned with this genus.

The similarities with *G. clavigera* also include *Asterophilia* within the new subfamily Arctonoinae wherein it can be distinguished from most of the genera by its relatively short body and elytron attachment pattern. Some species of *Adyte*, *Subadyte*, and *Paradyte* could be confused with *Asterophilia* because they have 15 or 16 pairs of elytra and the same attachment pattern (for the first 15 pairs). However, all these species have well-developed semilunar pockets on all neurosetae (see remarks under *A. carlae* below).

Asterophilia carlae sp.nov.
(Figs 13A-G, 14A-G, Plate 1C-F)

Type material. HOLOTYPE - NTM W5265, Fiji, Mana Western, from oral side of *Linckia laevigater*, 5m, July, 1985, coll.?.

Additional material. ZMA V.Pol.319 Gier No. 3, Exp. No. 26, Wit oksels des armen van en Astrides, 25.x.1907, 2 specimens.

Description. *Holotype*: Body flattened, fusiform, fragile, flesh-coloured. Length 11mm, width including parapodia 4mm. 35 segments.

Elytra 15 pairs on segments 2, 4, 5, 7, alternate segments to 23, 26, 29 and 32. Elytra large, soft, overlapping medially and posteriorly, covering dorsum. Elytra without tubercles or fringe of papillae, with fold on anterior edge near elytrophore scar (Figs 13D, 14B), posterior margin sometimes slightly folded or convoluted, posterior half of elytra with three, rarely two or four, raised domes, not easily visible on preserved specimen. Most of elytron transparent but domed areas with creamy, white pigmentation (Plate 1D-F).

Prostomium bilobed, wider than long, without cephalic peaks (Figs 13A, 14A). Two pairs of eyes, anterior pair of moderate size, lying dorsolaterally at widest part of prostomium, posterior pair slightly larger, close behind anterior pair and closer to midline. Palps, short, stout with abruptly tapered tips. Median antenna with moderate sized ceratophore inserted in anterior notch, with style smooth, basally cylindrical, expanding into very large subterminal inflation and abruptly tapered short, filiform tip; lateral antennae with distinct ceratophores, shorter and thinner than median ceratophore, inserted termi-

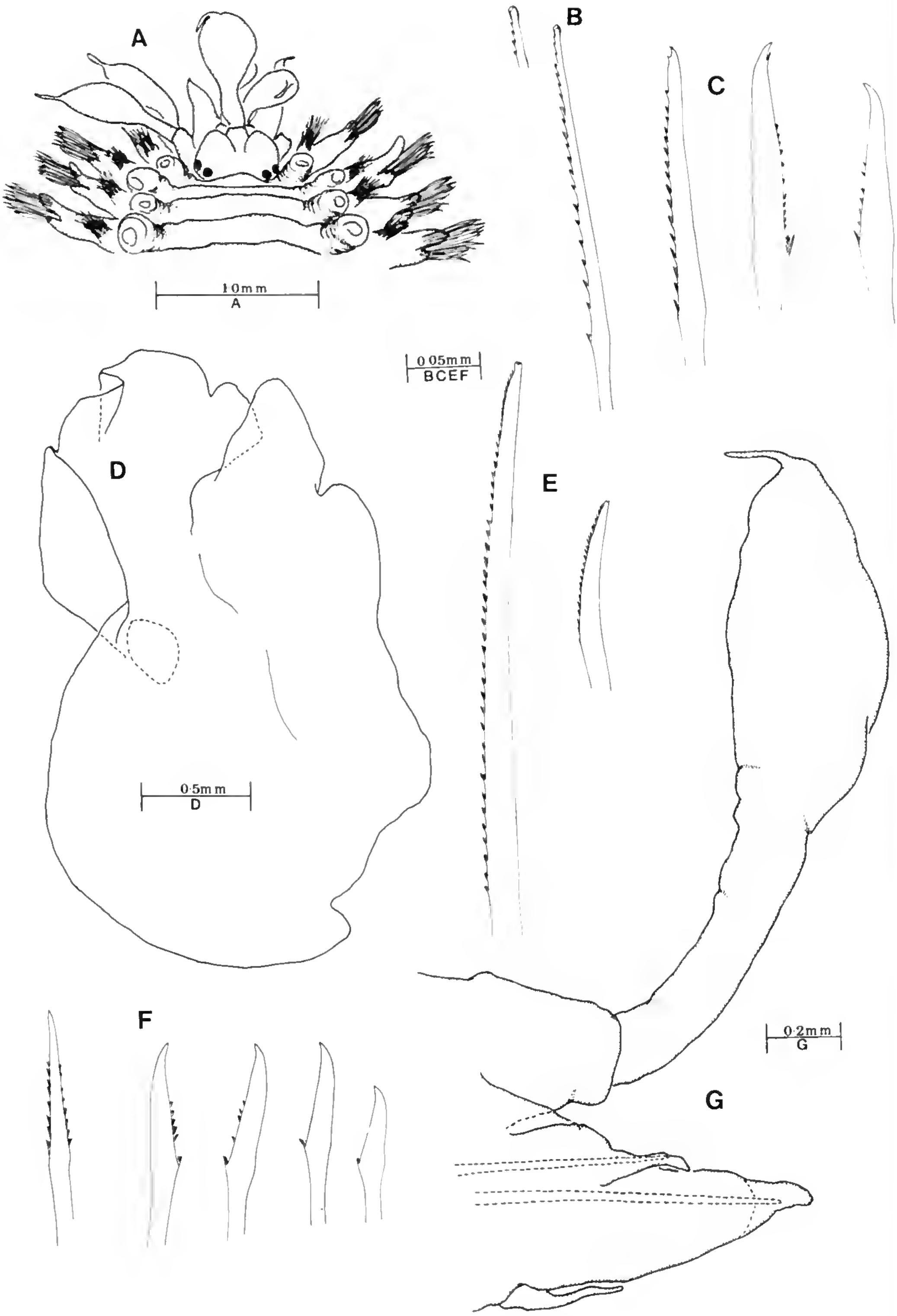

Fig. 13. *Asterophilia carlae* holotype: **A**, anterior end, dorsal view; **B**, upper neuroseta; **C**, middle neurosetae; **D**, elytron; **E**, notosetae; **F**, middle and lower neurosetae; **G**, cirrigerous parapodium, posterior view.

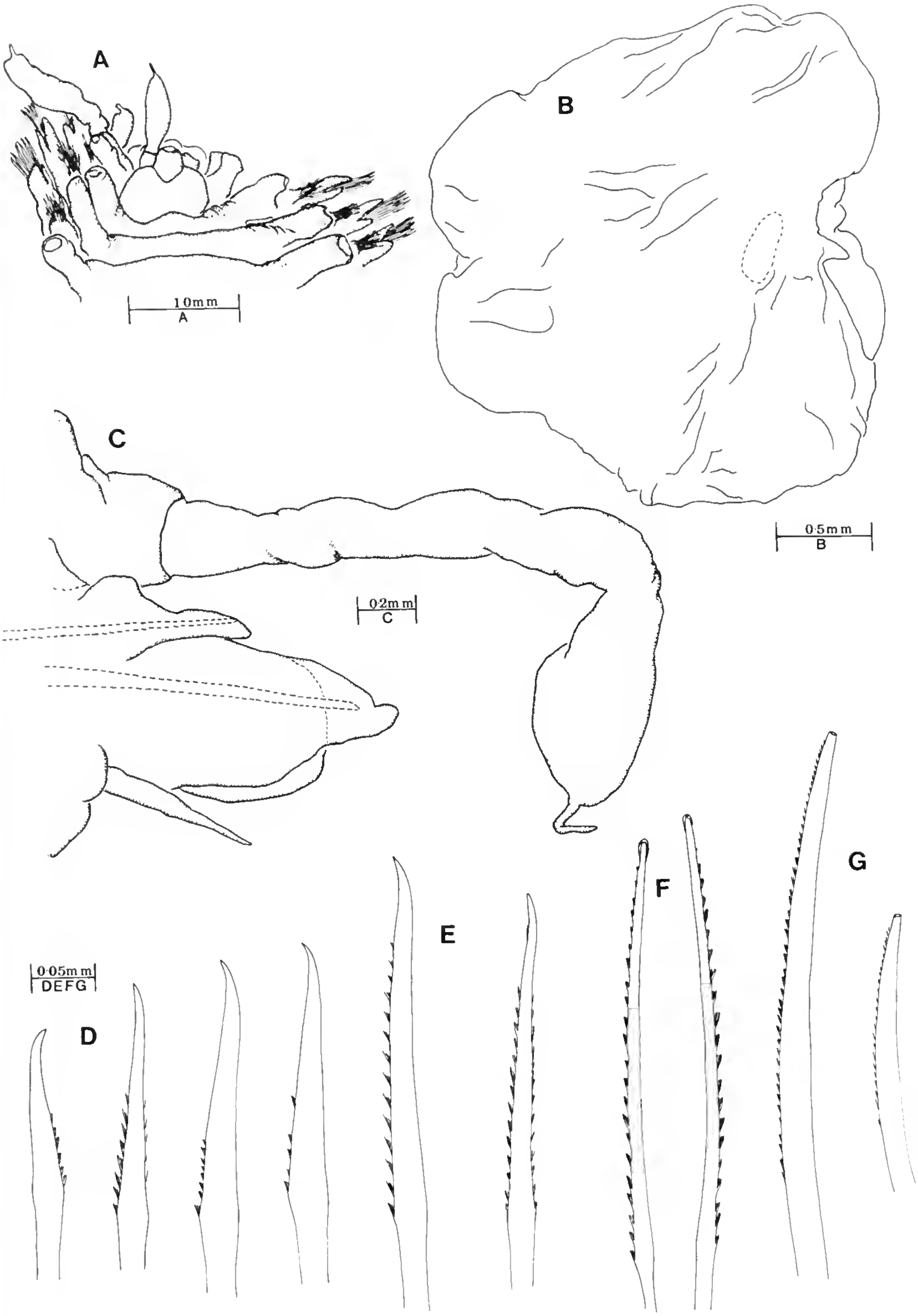

Fig. 14. *Asterophilia carlae*, two specimens from Gaspar Strait, **A**, larger specimen, **B-G**, smaller specimen: **A**, anterior end, dorsal view; **B**, elytron; **C**, anterior view of cirrigerous parapodium; **D**, lower neurosetae; **E**, middle neurosetae; **F**, upper neurosetae; **G**, notosetae.

noventrally on prostomium (Figs 13A, 14A), converging midventrally on the underside of the prostomium, styles similar in shape to median antenna but much shorter.

Tentacular segment, not visible dorsally, tentaculophores of moderate length lateral to prostomium, achaetous, with two pairs of dorsal and ventral tentacular cirri; styles smooth, of similar length and form to median antenna. Facial tubercle weakly developed. Segment 2 with semilunar nuchal fold, first pair of large elytrophores, subbiramous parapodia, and ventral buccal cirri with styles of similar length and shape to lateral antennae.

Parapodia subbiramous (Figs 13G, 14C). Notopodium small, subconical, with long, digitiform acicular lobe, on anterodorsal side of neuropodium. Neuropodium much larger (Figs 13G, 14C) with longer subtriangular presetal acicular lobe with a sharply rounded tip, and shorter, bluntly rounded postsetal lobe.

Notosetae (Figs 13E, 14G) short to long, curved, with rows of serrations along outer edge and notched tips (Figs 13E, 14G). Upper neurosetae long, slender with a subdistal swelling, many rows of serrations and hooded, notched tips (Figs 13B, 14F); middle neurosetae stouter, with pronounced subdistal swelling, fewer rows of serrations, most basal largest, resembling semilunar pocket seen on specimens of *Adyte*, and bi- or unidentate tips (Figs 13C, F, 14E); lower neurosetae, stout, shorter, with subdistal swelling, few rows of serrations and unidentate, slightly curved tips (Figs 13F, 14D); neurosetae in middle of bundle grading from upper to lower types.

Dorsal cirri on segments without elytra, cirrophores large cylindrical, with styles large, basally cylindrical, expanding into large subterminal inflation and abruptly tapered filiform tip (Figs 13G, 14C). Ventral cirri short, gradually tapering to filiform tip. Nephridial papillae well-developed, conspicuous, beginning segment 6 and continuing to end of body.

Pygidium small, terminal, with pair of anal cirri similar to dorsal cirri.

Holotype commensal on large blue starfish *Linckia laevigater* (Plate 1C).

Description of two specimens, from Gaspar Strait on asteroid: Both incomplete, one with 27 segments, length 19mm, width including parapodia 4.8mm; the other with 20 segments, length 10mm, and width including parapodia 4.4mm. Prostomium of larger specimen (Fig. 14A) lacking eyes, only left antenna and ventral tentacular cirrus remaining, both palps missing, otherwise similar to holotype. Prostomium of smaller specimen with two pairs of eyes and similar to holotype except for pair of long, slender palps considerably longer than those of holotype.

Parapodia and setae of specimens also similar to those of holotype (Fig. 14C-G). Larger specimen lacking elytra, a few remaining on smaller specimen (Fig. 14B); pattern of attachment on incomplete specimens identical to holotype.

Specimens recorded from the arms of asteroid by Horst (1917).

Distribution. Known only from the Type locality, Mana Western, Fiji and the Gaspar Strait, Indonesia.

Etymology. The species is named after my daughter Carla in honour of her 7th birthday.

Remarks. *Asterophilia carlae* when first observed on the host, the large blue seastar *Linckia laevigater* (Plate 1C) appears conspicuous (Plate 1D-F), seemingly incongruous, since in general, the match of colour pattern and shape between commensal and host is by necessity excellent - testament to the eyesight of predators. It appears to me that the polynoid is in fact beautifully mimicking the tube feet of its starfish host. Often the seastar has only a portion of each ambulacral groove open and this groove, through which the tube feet protude, is ellipitical in outline. *Asterophilia carlae* mimics such an opening in an ambulacral groove perfectly because the large swellings on the ends of its antennae, tentacular and dorsal cirri, and the three raised mounds on the posterior edge of each elytron resemble closely the tube feet of the seastar (Plate 1D-F).

The two specimens of *A. carlae* collected by the Siboga expedition (Horst 1917) were also collected from a starfish, however the species of host was not recorded.

Linckia laevigater (Linnaeus, 1758) is widely distributed throughout the Indo-Pacific region (Clark and Rowe 1971) where it can be found in large numbers on coral reefs. Given the wide distribution and large numbers of this host it is surprising that *A. carlae* seems to be rare. Dr Paddy Ryan (pers.comm.) has informed me that although *L. laevigater* is common in nearshore waters of Fiji, he has

seen very few specimens of *A. carlae*. During a recent expedition to Ashmore and Cartier reefs by staff of the Northern Territory Museum, a comprehensive examination of several hundred specimens of *Linckia laevigater* failed to find a single polynoid commensal.

I have not described the basal row of spines on the neurosetae of *A. carlae* as semilunar pockets (Fig. 13B, C, F). They are not as well-developed as those seen on species of *Adyte* and related genera (Pettibone 1969a; Hanley 1984), and I am not convinced they are homologous, although given the placement of *Asterophilia* and *Adyte* in the same subfamily on other morphological grounds, they may well be.

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REVISION OF *PALMYRA* SAVIGNY (POLYCHAETA:APHRODITIDAE) AND REDESCRIPTION OF *PALMYRA AURIFERA*

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ABSTRACT

The polychaete genus *Palmyra* Savigny is revised; *P. aurifera* is redescribed and illustrated from museum and recently collected specimens from coral atolls and volcanic high islands of the Indo-Pacific. Relationships of the genus with members of the family Chrysopetalidae and Aphroditidae are discussed and reassessed based on characters examined in the present study. *Palmyra* is now placed in the family Aphroditidae, superfamily Aphroditacea.

KEYWORDS: Polychaeta, Aphroditidae, *Palmyra*, systematic relationships, Indo-Pacific.

INTRODUCTION

The genus *Palmyra* Savigny has had a confused taxonomic history. The genus has been variously included in the family Aphroditidae, Palmyridae and Chrysopetalidae. More recently, Day (1967) included the Chrysopetalidae in the Palmyridae. In view of the uncertainty, and as a part of my on-going study of the systematics of the family Chrysopetalidae (Watson Russell 1986, in press), clarification of the taxonomic status of the genus *Palmyra* is necessary. Relationship of the palmyrids to the family Aphroditidae has been suggested by a number of authors (e.g. Savigny in Lamarck 1818; Audouin and Milne Edwards 1832; Racovitza 1896; Grube 1878; Augener 1913, 1922; Pettibone in Perkins 1985). In this paper a comparison of the morphology of the palmyrids and aphroditids is used to assess the systematic position of *Palmyra* within the Aphroditidae.

Only 13 specimens of *Palmyra* exist in museum collections. All of these specimens were examined following the methodology developed during investigation of chrysopetalid setal patterns (Watson Russell 1986, in press). Due to their larger size and because few *Palmyra* specimens were available for study, setal types on every segment were examined *in situ* under a dissecting microscope and only some smaller anterior and posterior segments were excised and mounted on slides.

Material examined was borrowed from the following institutions: Allan Hancock Foundation, University of Southern California, Los Angeles (AHF); British Museum of Natural History, London (BMNH); Hamburg Zoological Museum (HZM); Muséum National Histoire Naturelle (MNHN); Northern Territory Museum, Darwin (NTM); National Museum of Natural History, Smithsonian Institution, Washington (USNM); Zoological Museum Berlin (ZMB); Zoological Museum Copenhagen (ZMC); Zoologisches Institut der Universitat Wien, Vienna (ZUW).

HISTORICAL BACKGROUND

Lamarck (1818) first described the genus 'Palmyre' (= *Palmyra*) based on "Palmyre aurifere, Sav. Mss." (= *Palmyra aurifera* Savigny) and included it in 'Les Aphrodites'. Savigny's original manuscript description, dated 1809, was not published until 1820 (Hartman 1951:222). Savigny (1820:17, 1826:342) placed *Palmrya* as a genus within the tribe Aphrodites with a more detailed description than that given in Lamarck, and cited the original *Palmyra aurifera* as a "nouvelle et fort belle espècè" from the Isle de France, Mascarenes (= Mauritius). He also recorded another palmyrid specimen as "*N. palmifera* Cuv., Collect." from the Red Sea, as communicated to him by M. Cuvier. I have not been able to find any further reference to the specimen either in the literature or in the MNHN collections.

Blainville (1828:462) gave a brief description of *P. aurifera* and remarked on its similarity to that of the aphroditid group Hermiones. Audouin and Milne Edwards (1832:445, pl. 10, figs 1-6) included "le genre Palmyre de M. Savigny" within the tribe 'Aphrodisiens Nus' and referred to it as being distinguished from all other aphroditids by the absence of elytra and its similarity to members of the tribe Hermione. They also figured the species for the first time.

Grube (1850) briefly mentioned *Palmyra aurifera* and suggested it had similarities to the scaleworm *Eumolphe fragilis* Risso and the amphinomid *Spinther oniscoides* Johnson. Later, Grube (1855) described a small paleae-bearing polychaete from the Mediterranean as *Palmyra debilis* (= *Chrysopetalum debile*).

Kinberg (1858) created the Palmyracea as a family within the Aphroditea and defined it as lacking elytra; paleae on all segments; tubercles and dorsal cirri alternating. Schmarda (1861) placed *Palmyra* and his newly named genera *Paleanotus* and *Bhawania* in the family Palmyracea Kinberg. Claparède (1864) further described two small paleae-bearing forms from the Mediterranean: *Palmyra (Palmyrides) Portus Veneris* and *Palmyra (Palmyropsis) Evelinae*, as "deux Aphroditacés nouveaux du genre Palmyre". Examination of the descriptions of these species establishes that they belong to the Chrysopetalidae. Quatrefages (1865) included *Palmyra* and Schmarda's new genera in the family Palmyriens.

Ehlers (1864) erected a new family, Chrysopetalea (= Chrysopetalidae) to contain his new genus *Chrysopetalum*, *Paleanotus* Schmarda, *Bhawania* Schmarda, and questionably, *Palmyra* Savigny. In a paper entitled "Bemerkungen über die Familie der Aphroditeen" Grube (1875) briefly discussed the problematic placement of *Palmyra*. He initially agreed with Auduoin and Milne Edwards's separation of the aphroditids into the scaled and naked genera, the latter containing *Palmyra*. However, he suggested that Ehlers's family Chrysopetalacea, be united with Kinberg's family Palmyracea, and that the latter be excluded from the aphroditids. Grube (1878) later published a lengthy description of a specimen of *Palmyra aurifera* from Palau. He included *Palmyra* in the Palmyracea and remarked on its similarity to the aphroditid genus *Pontogenia* Claparède.

In his study on the anterior end of *Chrysopetalum debile*, Racovitza (1896) came to the conclusion that it was impossible to unite *Chrysopetalum* and *Palmyra* (*sensu* Savigny) in the same family and remarked that *Palmyra* was perhaps a true cousin of the aphroditid genera *Pontogenia* and *Aphrogenia* Kinberg.

McIntosh (1885) identified a specimen collected by the *Challenger* from off Japan, as *Palmyra aurifera*?. He described it as possessing scales and compared it with the genus *Pontogenia*. Potts (1910) described two palmyrids from the Indian Ocean as *Palmyropsis macintoshi* and *Palmyra splendens*.

Augener (1913, 1922) offered a comprehensive review of *Palmyra aurifera* and made detailed reference to specimens of *Palmyra aurifera* collected from the Kingsmill Is (= Gilbert Is). In his 1913 paper, Augener designated McIntosh's *Challenger* specimen as 'non *Palmyra aurifera*' and considered it better placed in the aphroditid genus *Pontogenia* or *Aphrogenia*. In an extensive footnote Augener (1922:9-10) questioned the validity of Potts's species, and after noting the preoccupation of the name *Palmyropsis*, considered that both species should be referred to *P. aurifera*. My examination of McIntosh's and Potts's type-specimens in the BMNH confirms Augener's view. Augener pointed out that past confusion had led to an amalgamation of *Palmyra* with the smaller paleae-bearing chrysopetalid genera, and suggested that since *P. aurifera* obviously did not fit into the family Chrysopetalidae, then either the characters of the family Palmyridae should be emended or the monotypic genus *Palmyra* be incorporated into a new family for which he suggested the name Gymnaphroditidae, to be placed as a subfamily of the Aphroditidae. Horst (1917) maintained a similar view and suggested that *Palmyra* and *Palmyropsis* be included in Augener's proposed Gymnaphroditidae.

Subsequent workers did not adopt Augener's nomenclature. Chamberlin (1919) recognised the separate identities of the Chrysopetalidae and Palmyridae, and included *Palmyra* and *Palmyropsis* Potts in the latter family. Monro (1924) re-examined

McIntosh's *Challenger* specimen, placed it in the genus *Pontogenia* and, together with additional specimens collected from the China Sea, described it as a new species, *P. macintoshi*. Specimens in the BMNH, collected from New Britain, and represented only by a number of incomplete parapodia on slides, were labelled with unpublished names by Willey as '*Palmyra aurifera, Palmyra aurifera squamata* and *Palmyra japonica*'. As far as I can determine, all of these parapodia belong to the aphroditid genera *Pontogenia* and *Aphrogenia*.

Hartman (1954:631, fig. 174A) described four specimens from the Marshall Is. and figured the anterior end of *Palmyra aurifera*. In her Catalogue, Hartman (1959:125) cited the two families separately as Palmyridae and Chrysopetalidae. Day (1967:115) synonymised Chrysopetalidae with Palmyridae and the genus *Chrysopetalum* with *Paleanotus*.

Mileikovsky (1977) placed both families in the order Phyllodocemorpha. Fauchald (1977) listed the two families separately under the superfamily Chrysopetalacea within the suborder Aphroditiformia, order Phyllodocida; Ushakov (1982) listed the two families in a similar manner to Fauchald, within the order Phyllodocemorpha. Pettibone (1982) made no reference to the palmyrids but cited the Chrysopetalidae as an aberrant family in the superfamily Aphroditacea. However, Perkins (1985) quotes Pettibone (in litt.) as including *Palmyra* in a subfamily of the Aphroditidae.

SYSTEMATICS

Superfamily Aphroditacea Johnson, 1839

Family Aphroditidae Malmgren, 1867

Description (after Pettibone 1966, 1982, in part - emended to include genus *Palmyra*). Body relatively large, broad, ovate or oblong; flattened ventrally, arched dorsally; less than 60 segments. Epidermis entirely or partly covered with small to large tubercles. Prostomium and segment 1 non-retractile or retractile within anterior segments (*Palmyra*). Prostomium subovate with sessile eyes or eyes on rounded or club-like ocular peduncles; single median antenna, comprising basal ceratophore and style; pair of long, smooth or ciliate ventral palps. Papillated facial tubercle ventral to median antenna, anterior to mouth, present or absent (*Heteraphrodita*). First or tentacular segment projecting anterolaterally and fused in part to prostomium, with 2 pairs of tentacular cirri and uniramous lobes with paleae and/or capillary setae. Following parapodia biramous, supported by 1 or 2 aciculae, with longer dorsal and shorter ventral cirri; cirri with clavate tips. Buccal or second segment with long ventral cirri lateral to mouth. Eversible pharnyx elongate, muscular, with papillae around opening and non-chitinous plates; intestine with segmental caeca. *Aphrodita, Laetmonice, Pontogenia, Aphrogenia* and *Heteraphrodita* with 13-20 pairs of elytra located on segments 2, 4, 5 and 7, continuing alternately to segments 23 or 25, then on every third segment to posterior end; long dorsal cirri present on segments lacking elytra. Elytrophores large, transversely elongate, thin-walled. Dorsal tubercles, corresponding in position to elytrophores on cirrigerous segments, transversely elongate, large, thin walled, with single or fimbriated papilla in medial-posterior position (*Aphrodita, Laetmonice, Pontogenia, Aphrogenia, Heteraphrodita*). *Palmyra* lacking elytra, elytrophores, dorsal tubercles or papilla; notopodia raised, elongate ridges with notosetal paleal fans on every segment; single paleal fans, numbering 13 pairs, on segments 2, 4, 5, 7-25; double paleal fans and dorsal cirri on segments 3, 6, 8, continuing on alternate segments to 26, thereafter on segments 27, 29, 30, 32, 33. Notosetae simple, of several kinds: main notosetal fan of stout, erect spines (*Aphrodita*), some with barbed or harpoon shaped tips (*Laetmonice*) or flattened paleal setae curving over the dorsum with or without serrated margins (*Palmyra, Pontogenia, Aphrogenia*), or main notosetal fan absent (*Heteraphrodita*); capillary setae extending dorsally forming feltage, covering elytra (*Aphrodita, Heteraphrodita*, some species of *Pontogenia* and *Laetmonice*); iridescent, laterally produced capillary setae (*Aphrodita, Heteraphrodita*) and/or short or long lateral capillary setae with varying degrees of development. Notosetal types alternate (*i.e.* presence/absence) in all genera except *Palmyra*. Neuropodia conical, with many tiered or relatively few stout, dark

simple neurosetae; numerous lower bipinnate neurosetae present on segments 2 and 3 (*Palmyra*, *Pontogenia*, *Aphrogenia*, *Laetmonice*, *Aphrodita*) or absent (*Heteraphrodita*); additional neurosetal types found in anterior and/or posterior segments of *Laetmonice* and *Aphrodita*. Pygidium very small and rarely visible in posterior segments.

Characters distinguishing palmyrids and chrysopetalids. The palmyrids and chrysopetalids are two distinct groups with major differences of the anterior end, setal types and their arrangement on the body, and overall body shape and size.

The prostomium of palmyrids is of the aphroditid type with a long biarticulate median antenna, eyes on club-like peduncles, two long, tapered palps and a large facial tubercle situated in an anteroventral position. The prostomium of chrysopetalids is composed of a short median antenna, two lateral antennae, two cylindrical or ovoid palps, sessile eyes and a dorsal nuchal organ. The form of the chrysopetalid prostomium has some similarities to those of syllid and hesionid polychaetes.

Palmyrids are large, broadly ovate worms with a tough tuberculate skin. Notosetae consist of stiff paleae in a rosette formation and small lateral fascicles of capillary setae; a small fascicle of simple neurosetae is present on all segments with additional bipinnate neurosetae on segments 2 and 3. Dorsal cirri and type of paleal fan alternate on mid-body segments. Chrysopetalids are small, elongate, and often very fragile. Setae consist of paleal and/or spinous notosetae (the former group inserted in a transverse row on the dorsum) and dense fascicles of compound neurosetae. There is no alternation of dorsal cirri and/or notosetal types; dorsal cirri and a similar type of paleal fan are found on all mid-body segments.

The one character that is immediately obvious and similar in both palmyrids and chrysopetalids is the possession of golden, notosetal paleal fans that imbricate down the dorsum. However, chrysopetalids possess paleae and spinous setae with an internally chambered box-like structure (Watson Russell, unpublished [paper given at the International Polychaete Conference, Sydney, 1983]; Perkins 1985). All other polychaete paleal types, including those belonging to *Palmyra* have an uncompartmented, longitudinally arranged, tubular type of internal structure.

In view of the differences in morphology of palmyrids and chrysopetalids and the similarities of the palmyrids and aphroditids, the family Palmyridae can no longer be included within the superfamily Chrysopetalacea. The Chrysopetalidae is retained as the single family within the Chrysopetalacea. Chrysopetalids share certain morphological and structural characteristics with the hesionid, syllid and nereid families of the superorder Nereidiformia. The systematic position of the family Chrysopetalidae will be elucidated in future papers.

Relationships of *Palmyra* within the Aphroditidae. Possession of dorsal cirri on alternate body segments (*i.e.* 3, 6, 8 etc.) allies *Palmyra* with the scaleworm families of the superfamily Aphroditacea. Relationship between the palmyrids and aphroditids (family Aphroditidae Malmgren, 1867) is indicated by a comparison of characters. Characters shared between *Palmyra* and other aphroditid genera are: (1) overall body shape with a limited number of segments; tuberculate skin; (2) similarity in overall shape, number and displacement of appendages and structure of the prostomium and segments 1 and 2; (3) overall shape of the elongate, muscular pharynx with papillate lip, intestine and segmental caeca; (4) possession of fascicles of large paleal or spinous notosetae that may alternate; (5) bipinnate neurosetae in anterior segments; (6) formation of developing oocytes along segmental blood vessels and their culmination in clusters around the segmental caeca; large, mature ova. Characters 1, 3, and 6 are also seen in variable states in other scaleworm families. The structure of the anterior end and the possession of fascicles of large, stout, notosetae that may alternate are characters shared at the family level by palmyrids and aphroditids. The family Palmyridae can no longer be sustained and it is therefore proposed that *Palmyra* be included as a genus within the family Aphroditidae, superfamily Aphroditacea.

Within the Aphroditidae *Palmyra* is most closely related to *Pontogenia*. Characters shared by these genera include: possession of paleae among setae of segment 1; a pattern of double and single paleae fans on the same

alternate segments (observed in palmyrids and two species of *Pontogenia*); capillary notosetae on all segments; palmyrid serrate paleae types similar to those seen in some *Pontogenia* species; clear distal 'cap' of cirri of *Palmyra* adults seen in juveniles and some adults of *Pontogenia*; posterior-most neurosetal types of young palmyrids seen in juvenile pontogeniids. *Palmyra* shares with *Pontogenia* and *Aphrogenia* the same type and number of adult neurosetae.

Characters defining the palmyrids are: retractile prostomium; tuberculate epidermis over the entire body; large, flattened paleae fans composed of broad, rounded paleae; alternation of notosetal types does not include presence/absence of any notosetal type; absence of eltyra, elytrophores and dorsal tubercles.

Origin and function of elytra and their absence in *Palmyra*. *Palmyra* differs from other known aphroditids in lacking elytra, elytrophores and dorsal tubercles. However, it is uncertain whether the absence of these characters are primitive or derived.

The Lower Cambrian fossil record includes forms with possible annelid affinities that possess imbricating mineralized scales (selerites of halkieriids - Jell 1981; Bengtson and Conway Morris 1984). The Burgess Shale material of the Middle Cambrian includes forms with flattened, paleae-like seales and erect spines (sclerites of wiwaxiids - Bengtson and Conway Morris 1984) and polychaetes with large notosetal fascicles of imbricating paleae (Conway Morris 1979). Jell (1981) ascribed a possible respiratory function to halkeriid sclerites but Bengtson and Conway Morris (1984) disagreed, suggesting that sclerites had a primarily protective function; they further hypothesized that the mode of respiration involved lifting of the sclerites to expose the dorsal surface in a manner analogous to that described for aphroditaccan polychaetes. Storch (1968) discussed the primary defensive/protective function of the large erect and flattened setae of the notopodia of certain polychaete families, Aphroditidae, Chrysopetalidae and Amphinomidae, that exhibited complex but primitive musculature.

From the fossil evidence it may be that fascicles of large notosetae (paleae and/or spines) and scales are primitive characters within the Polychaeta and in particular the Aphroditacea.

Reduction of the notosetal fascicle is seen in species of Aphroditidae that have alternating notosetal types, but complete loss of the large notosetal spines is exhibited only by *Heteraphrodita*. Reduction of the notopodium and elytra, and loss of notosetae also has taken place in certain commensal species of Polynoidae (R. Hanley personal communication).

The only other example of a scaleworm species in which elytra are absent is the aberrant interstitial sigalionid, *Metaxypsamma uebelackerae* Wolf, where the adult form retains neotenous characters. Wolf (1986) suggested that the absence of notopodia and eltyra in *Metaxypsamma* conferred a narrower body which allowed better exploition of interstitial spaces.

In scaled aphroditid genera the elytra serve to ensure the circulation of water over the thin-skinned dorsum which is considered to be the true respiratory surface (Fordham 1925; Van Dam 1940; Mettam 1971). Van Dam's opinion that during respiratory movements the elytra are depressed by muscular contraction of the elytrophores and elevated by coelomic pressure was supported by Mettam's study of the muscular anatomy of these structures. The elongate, thin-walled elytrophore on the elytragerous segment and the similar, thin-walled dorsal tubercle (with a single or fimbriated papilla) on the cirrigerous segment each contain the dorsal lobes of the segmental caeca. In aphroditids the dorsal sac of the caeca are multilobed and this may create a greater surface area for internal respiration.

Species of *Aphrogenia* and *Laetmonice*, which inhabit hard substrates, possess low-set elytrophores and dorsal tubercles (with fimbriated or simple papilla), variable capillary notosetal development, and felt that is poorly-developed or absent. Species of *Aphrodita* and *Pontogenia*, which burrow in soft sediments, possess larger, elevated elytrophores and dorsal tubercles (with a large fimbriated papilla), and well-developed notosetal fascicles of capillary setae and feltage. The larger, more raised elytrophores and dorsal tubercles allows a large volume of water to pass over the dorsum, while the large faseicles of capillary setae are effective filters.

On the other hand, juveniles of *Aphrodita australis* and *Pontogenia chrysocoma*, that have been collected from hard substrates in shallow water, lack elytra, elytrophores, dorsal tubercles and notosetal felt. At this early stage the major notosetal types (spines or paleae) are relatively large compared to the size of the body, and entirely cover the dorsum (Watson Russell in prep). The difference in the degree of development of the dorsal tubercle and papilla, elytrophore, and certain notosetal types between adults and juveniles of *Aphrodita australis* and *Pontogenia chrysocoma* may be linked to the particular respiratory requirements of their respective habitats.

Palmyrids are restricted to crevices in hard substrates in clear, well-oxygenated oceanic waters, and the absence of elytra may be linked to the respiratory regime of their habitat.

Little is known of the relationships of scale-worm families, and revision of other aphroditid genera is necessary before the phylogenetic position of *Palmyra* within the Aphroditidae can be elucidated.

Palmyra Savigny

Palmyra Savigny in Lamarck, 1818: 20 (type species *Palmyra aurifera* Savigny in Lamarck, 1818, by monotypy). Gender: feminine.

Palmyropsis Potts, 1910:326 (type species *Palmyropsis macintoshi* Potts, 1910, by monotypy).

Diagnosis. Body broad, rectangular; anterior and posterior segments slightly tapered. Maximum segment number less than 40. Thick epidermis with globular papillae covers body. Prostomium with median antenna; two pairs of eyes on raised peduncles; two long palps; large facial tubercle. Segment 1 fused to prostomium with 2 pairs tentacular cirri; short, erect paleae fascicle, 2 fascicles capillary notosetae. Prostomium, segment 1 retractile in anterior segments. Large, folded mouth opening posterior to palps; elongate muscular pharynx; intestine with paired segmental caeca. Large, flattened fascicles of broad paleae imbricate down and across dorsum covering it entirely or leaving partly bare medial strip; paleae of anteriormost and posteriormost segments with margins serrate, faintly serrate on distal tips only or non-serrated entirely. Lateral small notopodial lobes with capillary setae; capillary fascicles thick, sparse or absent. Double paleal fans and dorsal cirri alternate (on segments 6-26) with single paleal fans (on segments 7-25); dorsal cirri double up on posteriormost segments. Lower bipinnate neurosetae on segments 2 and 3; simple bidentate neurosetae from segment 2. Pygidium not visible.

Description. *Prostomium*: *Palmyra* possesses a small prostomium with a short to medium length median antenna inserted on a broad, papillate ceratophore mid-dorsally on the prostomium. Each eye is composed of a coalesced pair of eyespots on an extended or retracted peduncle. Two long tapering palps with minute hairs and an elongate, marginally papillate facial tubercle are present (Fig. 2A,B). The median antenna, tentacular cirri, dorsal and ventral cirri are all composed of two articles in tandem; both articles are narrowed proximally and inflated distally with a half-rounded, clear, lens-like cap most distally (Fig. 1K).

Peristomium - Segment 1: Uniramous segment 1 supports a pair of tentacular cirri and a small anterior fascicle of erect paleal setae and posterior fascicles of short, relatively broad capillaries (Figs 1A, 3A). Segment 1, in conjunction with the prostomium, can be retracted within the anterior segments so that only the tips of the prostomial and peristomial cirri are visible; it is in this position that the eye peduncles appear retracted.

Segments 2-6: Segment 2 (buccal segment), 3 and subsequent segments are biramous. The notopodia of segment 2 are directed anteriorly and support a small, almost circular paleal fan and a fascicle of capillary setae. The neuropodia are small, with a fascicle of slender bidentate setae and a small lower, dense or sparse fascicle of golden bipinnate setae (Fig. 3C,D); ventral cirri or buccal cirri, the same length as the tentacular cirri, are situated on large cirrophores on each side of the mouth (Fig. 2B). Segment 3 has similar, slightly larger notopodia than segment 2 and dorsal cirri; neuropodia possess bidentate and bipinnate fascicles of neurosetae and short ventral cirri. Segments 4 and 5 have paleal and capillary notosetal fascicles and no dorsal cirri; neuropodia have 4 stout, brown bidentate setae and ventral cirri. Segment 6 has

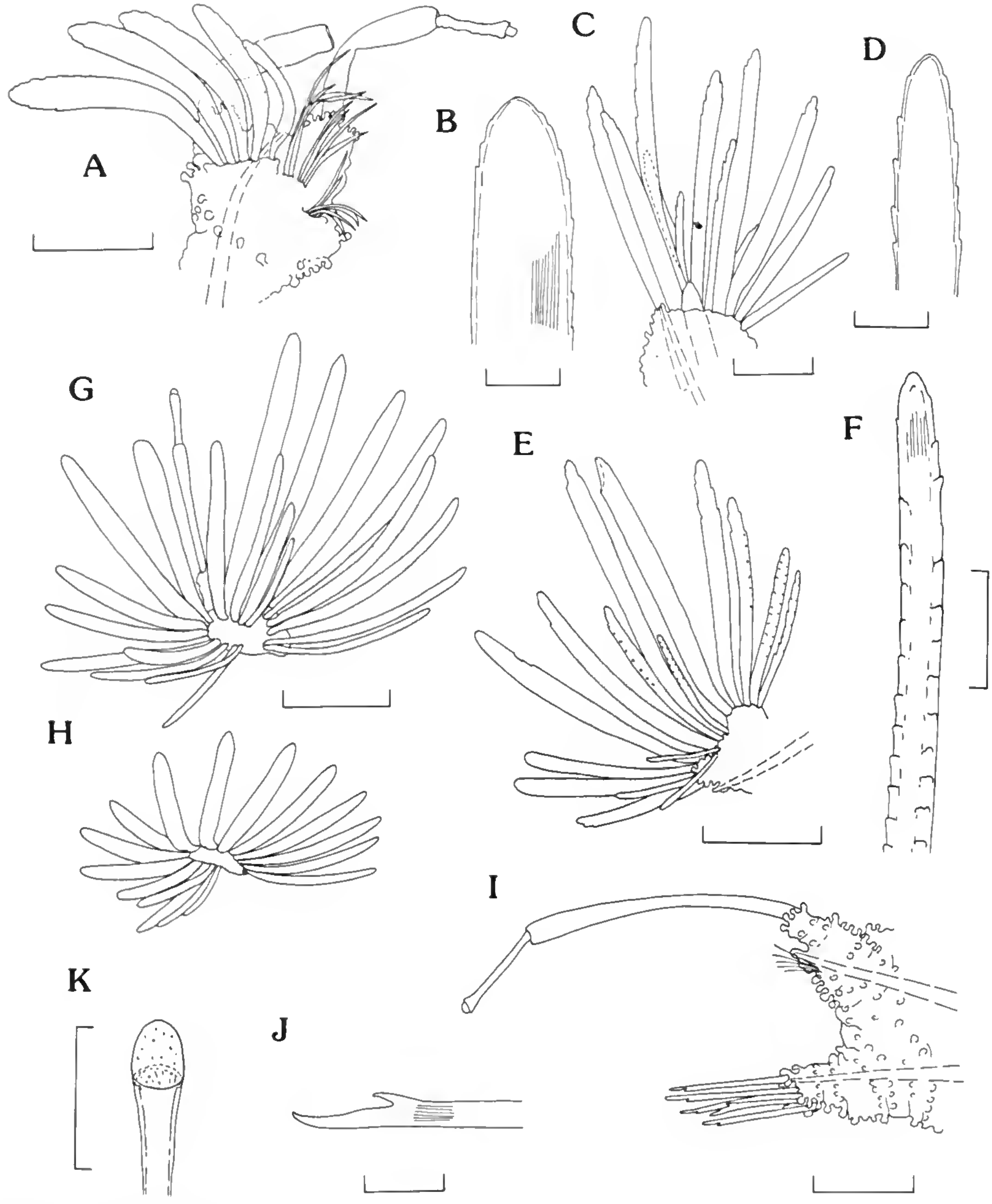

Fig. 1. *Palmyra aurifera* A-D,I-K, holotype MNHN UC92; E,F BMNH ZK 1224.3.1.149; G,H ZUW V.2180: A, parapodium from segment 1; B, detail of palea from same; C, notopodium from segment 29, anterior view; D, detail of palea from same; E, notopodium from segment 20, anterior view; F, detail of palea from same; G, double paleal fans of notopodium from segment 16, anterior view; H, single paleal fan of notopodium from segment 9, anterior view; I, parapodia from segment 29, anterior view, paleal notosetae not shown; J, detail of neuroseta from same; K, detail of distal end of dorsal cirrus from same. Acicula dashed A,C,E,I. Scales A,C,I = 0.4mm; B,D,F,J = 0.1mm; E,K = 0.2mm; G,H = 0.8mm.

notopodia with dorsal eirri and notosetae consisting of a lateral paleal fan with an overlapping medial fan; this arrangement is termed a 'double fan' (Figs 1G, 2H). Segment 7 has notopodia with no dorsal cirri and one paleal fan, termed a 'single fan' (Figs 1H, 2I). Paleal fans insert in a full or half rosette pattern in the notopodia.

Notosetae: Palmyrid paleae of midbody segments are long, symmetrieal with rounded

or pointed tips and smooth margins, pale golden to dark bronze-gold in colour. Several specimens have encrusting white, calcareous zooid organisms, resembling bryzoans, on the superior paleal surfaces; the same type of encrustation has also been observed on the ventral surface of worms. The notoaciculum is large and prominent within the notosetal fascicle. Double and single paleal fans are not well delineated in the anteriormost and posteriormost segments; the two posteriormost notopodia are very small with tiny setal fascicles. Paleal fans of the anteriormost and posteriormost segments have smaller numbers of paleae than those on the mid-body; single paleal fans have smaller numbers of paleae when compared with double paleal fans (Table 1, 2). The shortest paleae originate at lateral and medial points within the fan. All paleae have internal longitudinal striae and thickened margins. Capillary notosetae originate from a small, laterally positioned fascicle below the paleal fan and notoaciculum (Fig. 1I); they are often short and blade-like in the anterior segments (Figs 1A, 3A), becoming long and thin, with minute hairs in mid body segments. Capillary setal development is highly variable (Table 1, 2).

Alternation of notosetal types: Alternation of certain notosetal types involving presence/absence occurs in all aphroditid genera except *Palmyra*. The major palmyrid notosetal type (*i.e.* paleae) is present on all segments but double fascicles of paleae occur on the cirrigerous segments and single fascicles of paleae occur on the non-cirrigerous segments. The lateral capillary fascicle is present on all notopodia.

Neurosetae: Palmyrids possess one type of simple neurosetae from segment 4 onwards. Neurosetae are stout, bidentate, golden brown in colour and number 4 (Fig. 3I,K); in an exceptional case one neuropodium had 5 (Fig. 1I). A large dark brown neuroaciculum protrudes its distal tip into the neurosetal fascicle. Neurosetae of the posterior segments are paler in colour and more slender with elongate tips (Fig. 1I,J). All neurosetae have internal longitudinal striae and thickened margins. An additional small fascicle of bipinnate neurosetae is present in segments 2 and 3 in all palmyrid specimens (Fig. 3C,D).

Pharynx, Intestine and Caeca: Dissection of the palmyrid ventrum reveals the pharnyx, intestine and segmental caeca (Fig. 2C). The pharnyx is an elongate, maroon or pink coloured, muscular, flattened organ distally broad with a thick lip obscured by a membranous structure. Dissection of the pharnyx reveals the lip overlaid with a dense fringe of elongate, purple coloured papillae; a number of thick muscular protrusions, not horny or chitinous in any way, are located on the inner side of the lip. The pharnyx narrows proximally at the point of juncture with the thin walled intestine.

Segmental pairs of caeca arise at regular intervals from the dorsolateral sides of the intestine. In a 37 segment specimen (ZMC) 24 pairs were present, and a 30 segment specimen (AHF n.10159) possessed 18 pairs of caeca; in both worms the caeca started around segment 6 and ended about 6 segments from the posterior end. The anterior caeca are directed anteriorly on long necks (Fig. 2C); subsequent caeca have shorter necks and are directed laterally. The caeca of the former specimen were composed of a slender neck leading from the intestine to a large yellow coloured ventral sac. At the base of this sac, only visible in dorsal view, another short neck curved dorsally through a small space between intersecting muscle bands and, when teased out with forceps, is seen to end in a small dorsal sac that lies in the notopodial cavity (Fig. 2D). The 19th to 24th pairs of dorsal caecal sacs were bifurcated. The 30 segment specimen has large, blind ventral caecal sacs, coloured purple in part from its internal contents; there is no sign of the dorsal sac.

Epidermis: The thick, ridged epidermis of palmyrids varies in colour from grey to yellowish to an almost iridescent white. The segments are marked dorsally by raised, elongate notopodia which are joined by a narrow, raised ridge across the mid-body segments (Fig. 4I). There are breaks along this ridge between the notopodia of the posterior segments (Fig. 4J). In the medial area between the notopodial ridges of two segments are additional raised ridges. Shallower papillate ridges traverse the ventrum and form a circular pattern around the parapodia. The skin between these raised ridges and laterally between the notopodia is much thinner. Raised globular papillae have a canal that connects sub-dermally (Fig. 3J); they are conspicuous on all raised ridges and scattered across the thinner skin. The extensive folding of the

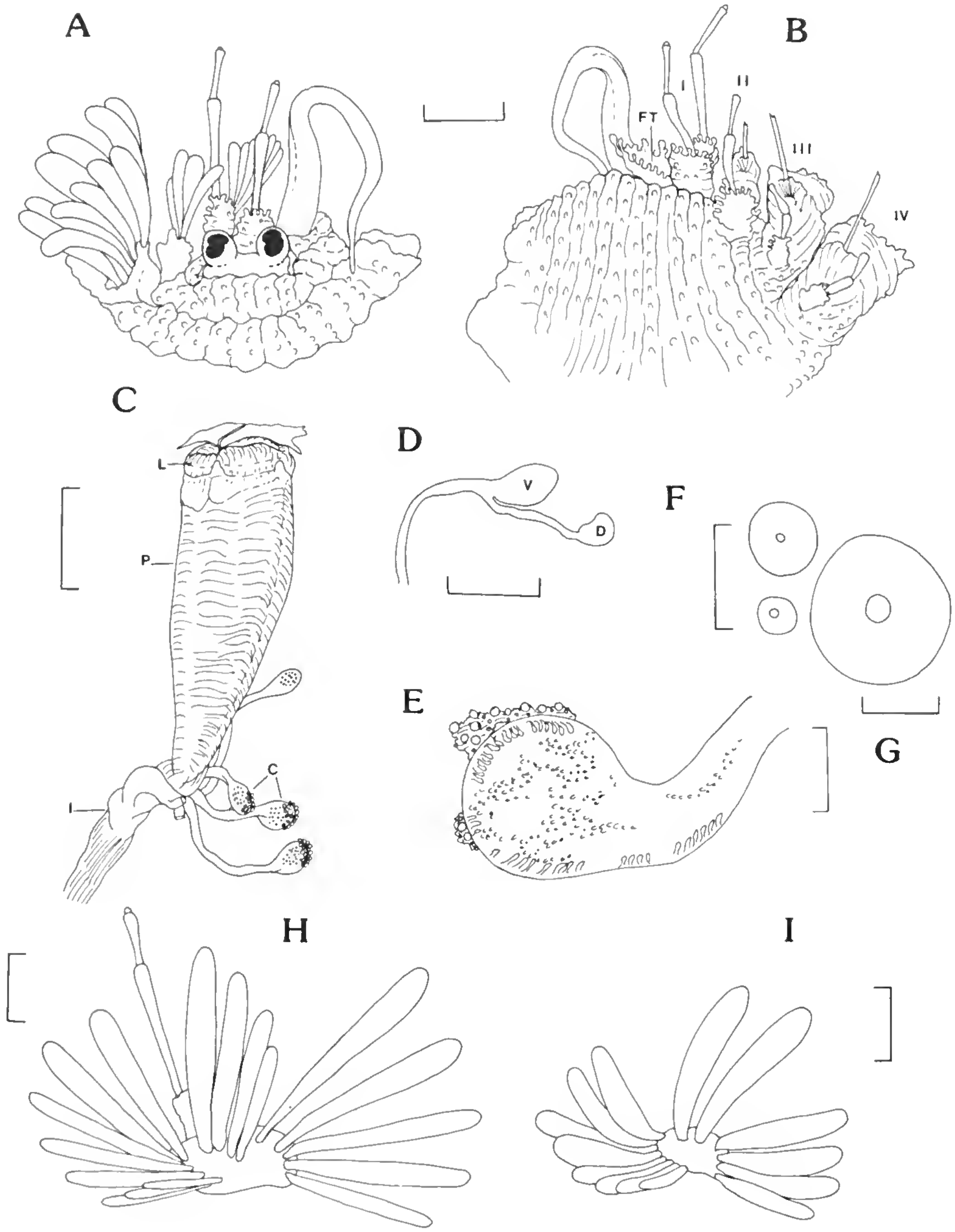

Fig. 2. *Palmyra aurifera* **A,B** USNM 29971; **C, E-I**, AHF n.10159; **D** ZMC: **A**, anterior end, dorsal view, paleal fan of left notopodium 3 pinned back to reveal prostomium, left palp and anterior 3 right parapodia missing; **B**, same, ventral view, paleae fans not drawn. Abbreviations: FT, facial tubercle; I, parapodia 1; II, parapodia 2,; III, parapodia 3; IV, parapodia 4; **C**, ventrolateral view with intestine twisted to view some of segmental caeca. Abbreviations: C, caeca; I, intestine; L, lip; P, pharynx; **D**, detail of caeca from segment 6, not in natural position, showing ventral sac (V) and dorsal sac (D); **E**, ventral sac with remains of egg cluster, detail of C; **F**, developing oocytes; **G**, mature egg from coelom; **H**, double paleal fans and dorsal cirrus of notopodium from segment 14; **I**, single paleal fan of notopodium from segment 5. Scales A,B = 0.4mm; C = 3mm; D = 1mm; E = 0.5mm; F = 0.1mm; G = 0.2mm; H,I = 0.6mm.

epidermis and the presence of papillae probably increases the respiratory surface area.

Biology. The reproductive biology of palmyrids is unknown. No palmyrid larvae or individuals under 28 segments have been reported. During dissection, I found large yolky eggs, 300-400μm in diameter (Fig. 2G), floating free in the coelom of *P. aurifera* (AHF n.10159). Developing oocytes of two sizes, 35μm and 60μm in diameter, were visible on the segmental blood vessels and terminated in clusters around the ventral caeca (Fig. 2E,F). In another specimen, developing oocytes measured 60μm and 170μm (HZM V.636). No nephridial papillae, such as those seen in other aphroditid genera have been observed in palmyrids although Grube (1878) reported "an opening on several rear parapodia on the abdominal side which probably correspond to the abdominal papillae of Polynoids". The large size of the mature eggs, at the top of the range for oocyte diameter observed in the Polychaeta (Olive 1985), suggests either an abbreviated non-feeding pelagic phase or direct development in *Palmyra*.

Remarks. *Palmyra* contains a single species (Tables 1 and 2 list and compare characters of 13 specimens). *Palmyra* is most closely related to *Pontogenia* within the Aphroditidae (see Relationships of *Palmyra* within the Aphroditidae).

A number of non-palmyrid species have been previously referred to the genus *Palmyra*: *Palmyra ocellata* Johnston 1827, has been synonymised with the sigalionid species *Pholoe minuta*; *Palmyra obscura* Müller 1858, was later included by Grube (1868) in his genus *Psectra* (based on Grube's description, specimens of *P. obscura* appear to belong to the chrysopetalid genus *Bhawania*); *Palmyra (Psectra)* sp.? of Ehlers (1887) from Florida is obviously a non-palmyrid as the given number of segments is 220; and *Palmyra? elongata* Grube 1856 from the West Indies belongs to the chrysopetalid genus *Chrysopetalum* (Perkins 1985).

Palmyra aurifera Savigny

(Plate IA,B, Figs 1A-K, 2A-I, 3A-K, 4A-J; Table 1, 2)

Palmyra aurifera Savigny in Lamarck, 1818: 305 [Ile de France, Indian Ocean]; Savigny 1820: 17; 1826: 341-342; Blainville 1828: 462-463; Audouin and Milne Edwards 1832: 445-446, Pl.10 Figs 1-6; Oken 1832: 942; Grube 1850: 286-287; 1875: 57-59; 1878: 12-15; Augener 1913: 80-83; 1922: 9-10; Chamberlin 1919: 92; Hartman 1954: 630, Fig. 174 A.

Palmyropsis macintoshi Potts, 1909: 370; 1910: 326, Pl.45 Fig. 18; Pl.46 Figs 21,22.

Palmyra splendens Potts, 1910: 327, Pl.20 Fig. 25, Pl.21 Fig. 34.

Type material. HOLOTYPE - Indian Ocean, Mascarenes, 'Isle de France'= Mauritius, MNHN UC92, coll. M. Mathieu, 1818. [Note: I examined the holotype in the MNHN in September, 1986. The vial containing the specimen has two labels: one label has a red border (denoting type) and the printed annotation 'Palmyra aurifera Sav. Ile de France. M. Mathieu. A (R) - 1868 - NO.45a.'; the other label has hand written in ink 'M. Mathieu (individu décrir par Savigny 1836, 1838)'. Dr Renaud-Mornant, Laboratoire des Vers, considers that the erroneous dates on both labels are "no doubt a misprint..."].

Additional material. WESTERN INDIAN OCEAN. Mascarenes: Mauritius, taken out of a hole in sponge, 100 fthms (182m), 1, BMHN ZK 1924 3.1.149, (holotype of *Palmyropsis macintoshi*), coll. Percy Sladen Trust Expedition, Indian Ocean, 1905; Cargados Carajos, Stn B2, 30 fthms (55m), 1, BMHN ZK 1924.3.1.80 (syntype of *Palmyra splendens*), coll. same as previous; Réunion I., 1, ZUW V2180.

EASTERN INDIAN OCEAN. Western Timor Sea: N.W. Australia, Ashmore Reef, under a piece of coal among coral rubble in shallow pool, on reef flat at low tide, 1, NTM W.5054, coll. R. Hanley, 15 April 1987.

PACIFIC OCEAN. Central Pacific: Marshall Is, Ifaluk Atoll, north of Klungalap, reef flats and coral heads, 1m, 1, USNM 29971, coll. Bayer et al, 4th Pacific Atoll Survey Team, Station 775, 28 October 1953; Enewetak Atoll, Lidilbut I., crevices of coralline algae, 2, AHF n.10159; Kingsmill Is = Gilbert Is, 1, ZMC (no registration number available), coll. Putze (note on back of label 'specimen probably purchased by Steenstrup from Putze, a German from Berlin who dealt with natural history specimens. Information from Jorgen Knudsen, July 1982 - M.E. Petersen'.); same locality and collector as previous, 1, ZMB 1282; Viti = Fiji, 1, HZM V637; Marquesas, Nukahiwa = Nuku Hiva, 1, HZM

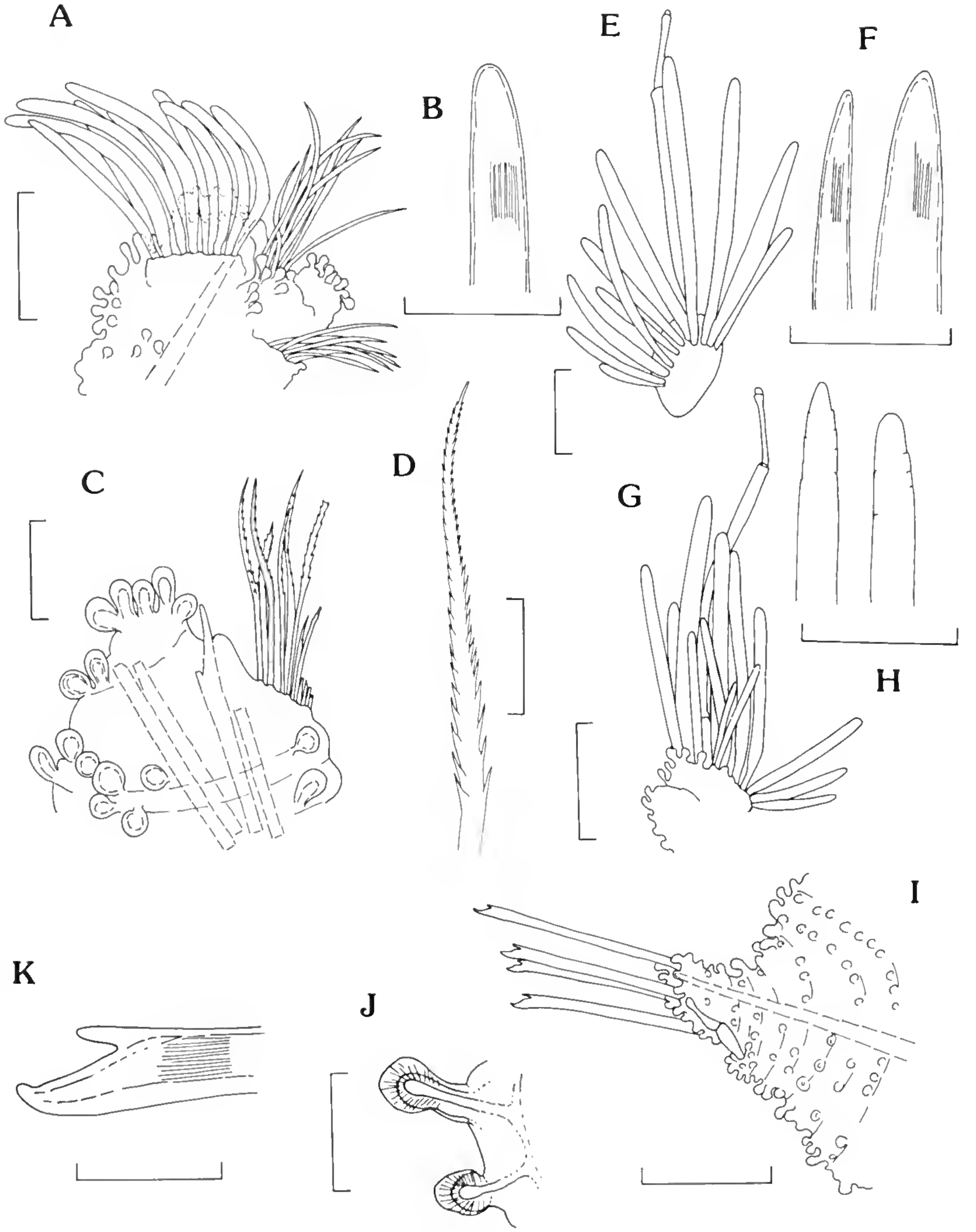

Fig. 3. *Palmyra aurifera* **A,B** ZMB 1282; **C,D** ZMC; **E,F** HZM V.636; **G,H** USNM 29971; **I-K** AHF n.10159: **A**, parapodium segment 1; **B**, detail of palea from same; **C**, neuropodium of segment 3, ventrolateral view, bidentate neurosetae dashed; **D**, detail of bipinnate neuroseta from same; **E**, notopodium of segment 36, anterior view; F, detail of paleae from same; G, notopodium of segment 34, anterior view; H, detail of paleae from same; I, neuropodium from mid-body, posterior view; J, detail of papillae from same; K, detail of neuroseta from same. Aciculа dashed in A and I. Scales A,I = 0.4mm; B,C,F,H = 0.1mm; E = 0.2mm; G = 0.5mm; D,J = 0.04mm; K = 0.05mm.

V636; Coral Sea, Chesterfield Reefs, 19° 14' S, 158° 30' E, in crevice of coral rubble block covered with algae, 32-52m, dredged, 1, NTM W.5138, coll. ORSTOM 1988 Chesterfield Reef Expedition, R. Hanley, 25 July 1988.

Description. Holotype entire, 30 segments, length 24mm, width 6mm. Broad, distally rounded paleae in fans, brassy golden in colour, imbricate dorsally; whitish encrustations present on ventrum. Long incision present on ventrum, pharynx entire inside. Prostomium and segment 1 partly retracted within segment 2. Median antenna on large ceratophore between two pairs of fused eyes on pedunculate ommatophores. Right palp entire, left palp damaged. Large convoluted facial tubercle clearly visible in ventral view, located between palps. Segment 1 small, reduced; notopodium uniramous with large aciculum; small erect fascicle of 5 paleae, 3 larger ones with serrate margins in part, 2 smaller ones with only distal tips serrate; 2 small groups of blade-shaped capillaries below paleae fascicle; long dorsal and ventral tentacular cirri (Fig. 1A,B). Segment 2 biramous; no dorsal cirri, ventral cirri with large cirrophores adjacent to mouth, styles broken; notopodium with small fascicles of paleae and capillaries; neuropodium with 2 types of neurosetae: 4 stout, golden-brown, bidentate, simple setae in superior position and lower, smaller fascicle of bipinnate setae; 2 acicula present in notopodia and succeeding segments. Segment 3 with notopodium possessing dorsal cirrus, fan of 13 paleae in 3 rows with shortest paleae proximally, and lower fascicle of capillaries; neuropodium with small ventral cirrus and 2 types of neurosetae as in segment 2. Segments 4 and 5 with paleal fans of 13 paleae each with 4 shortest in medial position; no dorsal cirri; neuropodium with ventral cirrus and 4 simple bidentate neurosetae as found in all succeeding segments. Neurosetae of segments 29 and 30 with slender, elongate tips (Fig. 1J) numbering atypically 5 on segment 29 (Fig. 1I), 4 on segment 30. Some paleae of posterior 2 segments with serrate margins in part (Fig. 1C,D). Dorsal cirri and double paleal fans alternate with single paleae fans on non-cirrigerous segments from segment 6-26. Pygidium not visible.

Comments on western Indian Ocean material. All specimens of *Palmyra aurifera* from the Mascarenes possessed paleae with some degree of serrated margins on the anterior two segments and on the posterior ten segments (Fig. 1B,D,F); the greatest degree of serration occurred in the smaller lateral and medial paleae of the fascicle. Potts's (1910:Pl.20, Fig. 25) figure of the second segment of *Palmyra splendens* (= *aurifera*) shows some distally serrate paleae. My examination of the posterior 3 segments of this same specimen showed similarly serrated paleae. Examination of *Palmyropsis macintoshi* (= *Palmyra aurifera*) showed the anterior paleae with serrations and also paleae within the posterior 10 segments (segment 20, Fig. 1E,F). The Réunion specimen also showed serrate paleae from segments 25-29.

Characters used by Potts as a basis for creating the new palmyrid genus, *Palmyropsis*, included sessile eyes and the almost complete lack of capillary setae. The specimen from Cargados Carajos, is one of the smallest palmyrids yet found (28 segments): it has smaller, 'finer' paleae fans of a much paler golden colour than those of larger worms. The anterior end is very retracted in this specimen and the globular eyes, which can only be seen in top view, appear sessile; this may be due to sudden contraction. The lack of capillary setae on some segments on this specimen is a condition also seen in some Pacific Ocean specimens; capillary development is a variable character observed both within and between individuals (Table 1, 2). An additional specimen belonging to *Palmyropsis macintoshi* was briefly described by Potts from the Seychelles "from a crack in a coral mass" at a depth of 37 fathoms (67m), and possessed a small capillary tuft on each segment. This specimen could not be located in the BMNH collections during a visit in 1986.

Potts (1910:Pl.21, Fig. 34) was the first author to figure the small lower bipinnate neurosetae on segments 2 and 3. They have been observed in all palmyrid specimens that I have examined.

Comments on eastern Indian Ocean and Pacific Ocean material. The paleal fans on the anterior, mid and posterior segments of specimens from the eastern Indian and Pacific Oceans showed some variability in the degree of serration on their margins. The young adult specimen from the Chesterfield

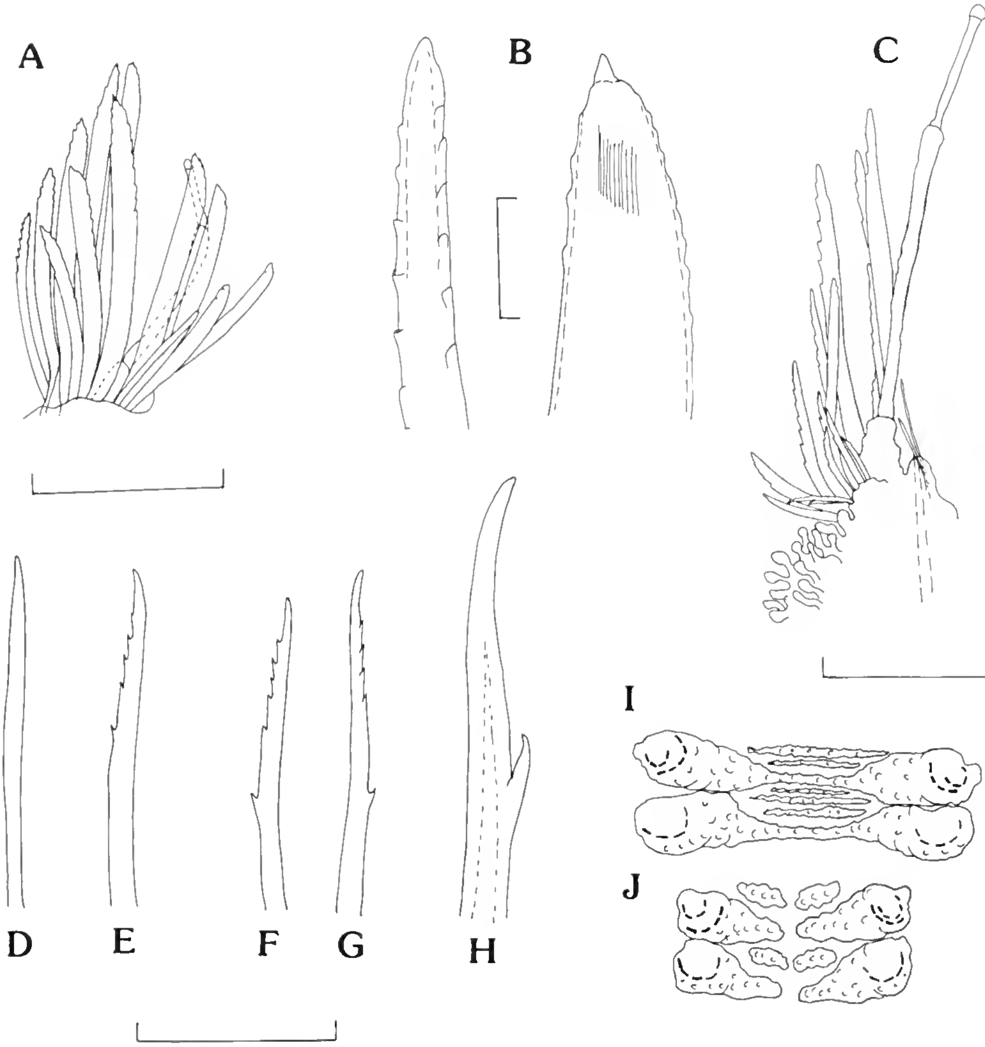

Fig. 4. *Palmyra aurifera* **A-H** NTM W.5138; **I,J** NTM W.5054: **A**, mid-body notopodium of segment 16, anterior view; **B**, detail of paleae from same; **C**, notopodium of segment 28, posterior view, aciculum dashed; **D-H**, neurosetal types from posterior 3 neuropodia; **I**, diagrammatic sketch of epidermal pattern on dorsum mid-body; **J**, same, posterior body, paleae insertion points dashed in I and J. Scales A,C = 1.00mm; B = 0.1mm; D-H = 0.04mm.

Reefs (NTM W.5138) possessed notosetal fans on all segments with nearly all paleae with some degree of serration on their margins (notopodium 16, Fig. 4A,B,C). Paleal fans of the posterior notopodia showed the greatest degree of margin serration on all paleae (notopodium 28, Fig. 4C). Paleae were long and slender; many with pointed tips (Fig. 4B).

Paleae with entirely smooth margins in notosetal fans on all body segments were found in adult specimens from Marquesas Is (HZM V. 636; notopodium 36, Fig. 3E,F), Fiji, two specimens from the Marshall Is and one specimen from the Gilbert Is (ZMB 1282; parapodium 1, Fig. 3A, B). Another Gilbert Is specimen of 37 segments (ZMC) possessed small paleae on segments 1 and 2 bearing minute serrations on part of the margin. A similar condition was present in the anterior and posterior most segments of one specimen from the Marshall Is (USNM 29971; notopodium 34, Fig. 3G,H). On segment 2 of the Ashmore Reef specimen (NTM W.5054) there were faint serrations on the smallest, lateral palea. On segment 29 of this specimen

Table 1. Comparison of characters of *Palmyra aurifera* specimens (Indian Ocean).

Institution	MNHN	ZUW	BMNH	BMNH
Reg. No.	UC92	V.2180	ZK 1924.3.1.80	ZK 1924.3.1.149
No. segments	30	29	31	28
Length (mm)	24	15	25	12
Width (mm)	6	8	9	6
No. paleae:				
Anterior seg. single fan	13	16	—	—
Anterior seg. double fan	13	—	—	—
Mid seg. single fan	15	17	14	—
Mid seg. double fan	18	18-23	—	16
Mid body capillary setae	sparse	sparse	sparse	sparse to absent
Ornamentation of paleae on posterior segments	serrate	serrate	serrate	serrate
No. neurosetae - mid segs.	4	4	4	4
Dorsal cirrus on segment no.	3,6,8...24,26,27	3,6,8...24,26,27	3,6,8...24,26,27,29,30,31	3,6,8...24,26,27

the 2 outermost paleae had minutely serrated tips. On segment 30 the 2 smallest innermost palea of a lateral fan of 5 were minutely serrated as was the innermost palea of the larger medial fan of 10 paleae (*i.e.* 3 tiny paleae had some margin serration compared with 12 smooth paleae in the same notosetal fascicle). Five specimens out of a total of 8 adult Pacific specimens, from a wide range of localities, possessed smooth, non-serrated paleae margins. While in three specimens a small degree of serration was retained in paleae fans of the anterior and posterior segments, the majority of Pacific adult palmyrids appeared to loose all traces of paleae serration with growth.

Neuropodia 27 and 28 of the young adult Chesterfield specimen (NTM W.5138) possessed a number of neurosetal types. A smooth small neuroseta (Fig. 4D) and distally serrate small neurosetae with and without a well formed spur (Fig. 4E,F,G) were two types not observed before in palmyrid specimens. Slender bidentate neurosetae (Fig. 4H) are typical of those seen in posterior segments of adult specimens (*cf.* Fig. 1J).

The prostomium and segment 1 are retracted in the Chesterfield specimen and the eyes retracted to the same degree as that observed in the Cargados Carajos specimen. One specimen in particular had a relaxed anterior end (USNM 29971); the prostomium and anterior 3 segments were visible (right 3 parapodia missing; Fig. 2A) as was the facial tubercle in ventral view between the long palps (left palp missing; Fig. 2B). The median antenna and tentacular cirri of this specimen are longer than those figured by Hartman (1954:631, Fig. 174a) for another specimen from the same locality. Differences in relative length of cirri was noted on a number of specimens, perhaps due to regeneration.

Size correlated to number of segments varies between specimens, and paleal colouration and capillary notosetal development are variable among Pacific island specimens (Table 2). The large Marquesas worm (HZM 636) (L 32mm, W 12mm and 37 segments), when compared with the Ashmore specimen (NTM 5054) (L 15mm, W 6mm and 30 segments), is more than twice as big. The former specimen has dark gold, stiff, robust, broad paleae; paleal fans do not interlock mid-dorsum, leaving it bare; capillary fascicles are small, stiff and sparse; and the epidermis is creamy coloured, very thick and conspicuously tuberculate. Paleae of the latter specimen are more slender and a pale gold colour with paleal fans just interlocking at the mid-dorsal line; capillary fascicles are feathery, bushy and comparatively longer; and the skin is pearly white and appears thinly opaque. Some of these differences (*e.g.* size, degree of robustness) may be due to age and/or sex but some characters, such as the degree of development of the capillary fascicle, is seen to be very variable both between and within individuals. The specimen from Fiji (HZM 637) has long, very well-developed capillary setae, numbering 30-40 on each segment. The two specimens from Enewetak Atoll (AHF 10159) are distinguished by a complete lack

Table 2. Comparison of characters of *Palmyra aurifera* specimens (Pacific Ocean).

Institution Reg. No.	NTM W.5054	HZM V.637	HZM V.636	ZMC	ZMB 1282	AHF n.10159	AHF n.10159	USNM 29971	NTM W.5138
No. segments	30	30	37	37	39	30	31	35	28
Length (mm)	15	15	32	20	31	25	27	25	10.5
Width (mm)	6	8	12	7	12	9	12	6	5
No. Paleae:									
Anterior seg. single fan	14-16	—	12	12	--	14	14	13	10
Anterior seg. double fan	14-16	14	12	12-15	--	14	15	14	12
Mid seg. single fan	18	18	13-16	13	14	14	13-14	14	12
Mid seg. double fan	20	20	14-17	15-17	--	--	17	16	13-15
Mid body capillary setae	mod. well dev.	well dev.	sparse	sparse to mod.	sparse to mod.	absent	absent	very sparse	sparse to absent
Ornamentation of paleae on posterior segments	minutely serrate	non serrate	non serrate	minutely serrate	non serrate	non serrate	non serrate	minutely serrate	serrate
No. neurosetae - mid segs.	4	4	4	4	4	4	4	4	4
Dorsal cirrus on segment no.	3,6,8...24, 26,27,29	3,6,8...24, 26,27,29	3,6,8...24, 26,27,29,30, 32,33,35,36	3.6.8...24,26, 27,29,30,32, 33	3...24,26,27, 29,30,32,33, 35,36,37	3,6,8... 24,26,27	3,6,8... 24,26,27	3,6,8...24,26,27, 29,30,32,33	3,6,8..24,. 26,27,28,

of capillary setae on any segment, although the small notosetal lobe is evident. The variability of this character between individuals of *P. aurifera* from the Indian and Pacific Oceans may be due to setal loss at a certain developmental stage and later regeneration, or loss perhaps due to environmental factors.

Grube's (1878) specimen of 37 segments, reported from Palau in the West Caroline Is, is not in the ZMB or HZM collections and appears to be lost. His description was general and included no figures. His observation of a brown pigmented patch on each segment next to the median line was not seen in the comparatively fresh Chesterfield or Ashmore specimens.

Remarks. Twelve of the palmyrid specimens fall into two geographically separate groups, distinguished by the degree of paleael serration on the anterior and posterior segments: in western Indian Ocean specimens distinct serrations are present on the paleae, but these are absent or only very weakly developed in the paleae of Pacific Ocean specimens. In view of the probable limited dispersal of palmyrid larvae and the very conservative morphology of the adults, I initially thought that two species might be present. However, a thirteenth palmyrid specimen, recently collected from the Chesterfield Reefs in the south-western Pacific by Russell Hanley, led me to question this conclusion. Unlike all other material, this specimen (NTM W.5138) has serrated paleae throughout the body. The Chesterfield specimen also is the smallest in size of all the palmyrids I examined, and has a number of characters that suggest it is a young adult. Sexually mature gametes were absent, and it possessed small numbers of paleae of the single and double notosetal fans. Certain setal types, not seen in more mature specimens, included slender, serrate, distally pointed paleae in most notosetal fans along the body, and smooth and serrate neurosetal types in the posteriormost segments.

Although paleal serration is much more developed in adults from the western Indian Ocean compared with adults from the Pacific Ocean, a correlation between body size and degree of paleal serration is not apparent between adults from the same region.

Until larger numbers of larval, juvenile and adult palmyrids from both regions can be collected and compared, I retain the species name *aurifera* for all specimens of *Palmyra*.

Distribution and Habitat. In the western Indian Ocean, *P. aurifera* is known only from the Mascarene Plateau, an area that consists of a series of submerged islands and shallow banks within the 1000 fathom line (Gardiner 1936), and includes the islands of Réunion, Mauritius, Caragados Carajos, and Seychelles. Réunion is a high volcanic island lacking coral reefs; Mauritius is volcanic, with

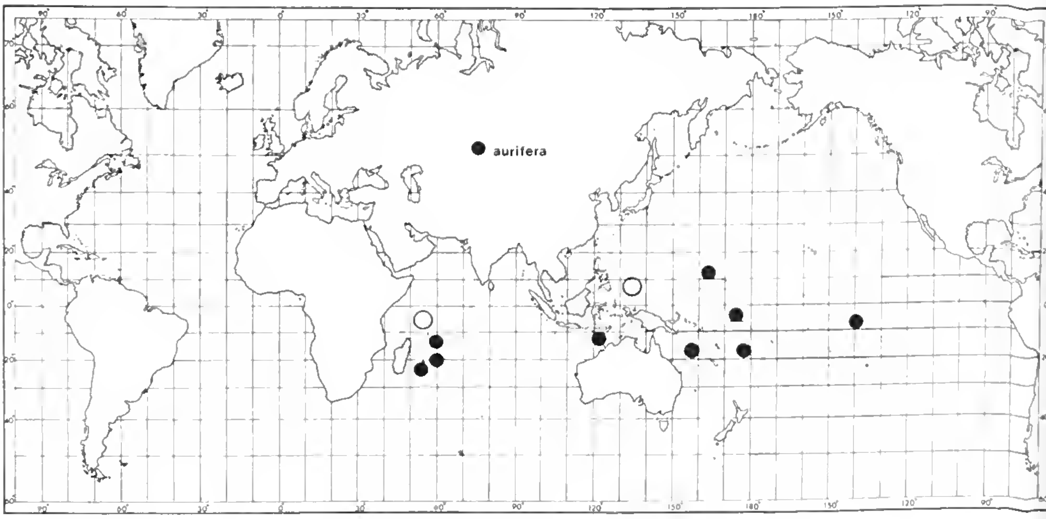

Fig. 5. Distribution map of *Palmyra aurifera*. Blank circle represents literature record only.

fringing coral reefs; Caragados Carajos consists of low-lying coral islands and sandy islets; and the Seychelles are of granitic origin, with fringing coral reefs.

In the eastern Indian Ocean, *Palmyra aurifera* has been collected from Ashmore Reef, off N.W. Australia. Ashmore Reef is a coral platform reef near the 200m line at the edge of the Sahul Shelf, an area close to the deep waters of the Timor Trough and the Wharton Deeps (Fairbridge 1950).

In the northern Pacific, *P. aurifera* occurs at Palau, Marshall Is, and Gilbert Is. The Palau group includes volcanic islands, coral atolls and submarine banks; the Marshall Is and Gilbert Is include coral atolls, islands, and raised and submerged banks.

In the south-western Pacific, *P. aurifera* has been collected at the Chesterfield Reefs and Fiji. The Chesterfield Reefs consist of coral atolls, and Fiji includes coral atolls and islands.

In the central Pacific *P. aurifera* occurs in the Marquesas, islands that are volcanic and lack coral formations.

Palmyra aurifera is largely restricted in its habitat to cracks and crevices in sponges, calcareous algae, and corals. In the western Indian Ocean, *P. aurifera* is known from depths down to 200m, but in the Pacific Ocean it occurs mainly in shallower waters to depths of 52m. In both the Indian and Pacific Oceans a common factor in the distribution of *P. aurifera* is the presence of well-oxygenated, clean, and sediment-free water.

ZOOGEOGRAPHY OF *PALMYRA*

The widespread but isolated pattern of distribution of *Palmyra aurifera* (Fig. 5) and its restricted habitat, suggest that *P. aurifera* may be a remnant species with a previous distribution that may have been much broader and included continental margins. Evidence in support of this is the occurrence of *P. aurifera* at Ashmore Reef, a platform reef at the edge of the Australian continental shelf, and the Seychelles, an old rafted continental fragment.

It is interesting to speculate that the present day distribution of *Palmyra* is the result of the breakup of Gondwanaland. I hypothesise that an ancestral aphroditid fauna was originally present along the shelf of Gondwanaland, and that part of the fauna was rafted northwards by the Indian plate, and north-eastwards by the Australian plate after the breakup of Gondwanaland in the late Jurassic (Seyfert and Sirkin 1973). At 75 myr the Seychelles, Saya de Malha Banks, and the Chagos-Laccadive group were adjacent to the west coast of India. Rupture of the Seychelles, Saya de Malha Banks, and the the Chagos group from India occurred during its drift northwards at a latitude of about 30°S during the early Paleocene (Davies 1968). The volcanic parts of the

Chagos-Laceadive Ridge and the Masearene Plateau were formed in the Eocene-Mioeene, with the location of the voleanos controlled by a transform fault. This enormous transform fault, was responsible for the separation of the Chagos archipelago from the Masearene Plateau during the formation of the Central Indian Ridge at 35 myr (McKenzie and Sclater 1971). Dispersal of palmyrids in the western Indian Ocean probably occurred southwards from the Seyehelles to Réunion, along the shallow banks and volcanic islands of the Masearene Plateau.

Palmyrids have very large yolky eggs which suggests a probable non-feeding pelagic phase or direct development and only a very limited ability to disperse. The present pattern of distribution of *P. aurifera* is consistent with the limited dispersal ability of an old remnant species.

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THE FIDDLER CRABS (OCYPODIDAE: *UCA*) OF DARWIN, NORTHERN TERRITORY, AUSTRALIA

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ABSTRACT

The colour patterns of live fiddler crabs and ontogenetic colour changes were documented in the field and compared with morphological results (particularly the shape of the male gonopods) obtained from a new collection. According to these studies the fiddler crabs of Darwin consist of nine species: *Uca capricornis* Crane, *U. dampieri* Crane, *U. elegans* George and Jones, *U. flammula* Crane, *U. hirsutimanus* George and Jones, *U. mjoebergi* Rathbun, *U. polita* Crane, *U. seismella* Crane, *U. signata* (Hess). The presence of additional *Uca* species, viz. *U. coarctata* (H. Milne Edwards), *U. dussumieri* (H. Milne Edwards) and *U. vomeris* McNeill reported by George and Jones (1982), is not confirmed here. These species appear to be confined to the east coast of Australia. It is also concluded that *U. pavo* George and Jones is a synonym of *U. capricornis* Crane: *U. pavo* represents an adult colour stage which was not adequately described in the original publication of Crane.

KEYWORDS: Brachyura, Ocypodidae, *Uca*, taxonomy, colour pattern, gonopods, Australia, biogeography.

INTRODUCTION

A study of the waving display and vibration signals of the fiddler crabs of Darwin, undertaken in July 1986 (von Hagen, in prep.) found only nine species of *Uca*, whereas 13 species have been recorded previously from this region (George and Jones 1982). The present contribution re-evaluates the systematics of *Uca* in the Darwin region, as presented in the George and Jones paper, and reduces the number of fiddler crab species known from the region from 13 to 9. The present paper provides a local faunal revision, and may be considered as a supplement to the booklet of George and Jones (1982), which will remain a general source of reference for all future students of Australian *Uca*. For this reason, full descriptions, full synonymies and older references are omitted. A key to the fiddler crabs of Darwin is presented for males and females, along with an annotated list of the nine species. The remarks contained in this list make use of the illustrations (Figs 2-5) that represent the main basis of the proposed corrections. In Figs 2 and 3 we follow the recommendation to give more weight to colour patterns of living individuals in systematic descriptions of decapods (Bruce 1975; Knowlton 1986). The drawings were prepared from colour slides and are thought to represent typical colour patterns of fiddler crabs from around Darwin, although variation across the ranges of species is not well documented. Scientific names are used in the usual simple binomial (genus, species), ignoring Crane's use of subgeneric names and subspecific ranking (for explanation see von Hagen 1976; Manning and Holthuis 1981; George and Jones 1982).

Material collected in 1986 and described here is lodged in the Zoology Collection of Marburg University (ZCMU). Additional material was provided by the U.S. National Museum, Washington (USNM), the Queensland Museum, Brisbane (QM), the Australian Museum, Sydney (AM) and the Western Australian Museum (WAM). Some of the specimens collected in 1986 are not included in the material listed here. These were left in the Northern Territory Museum, Darwin, as a reference collection. All measurements (given in mm) refer to the width of the carapace.

Abbreviations of species names are used throughout the synopsis of localities (see below) as well as in the legends of Figs 2-5.

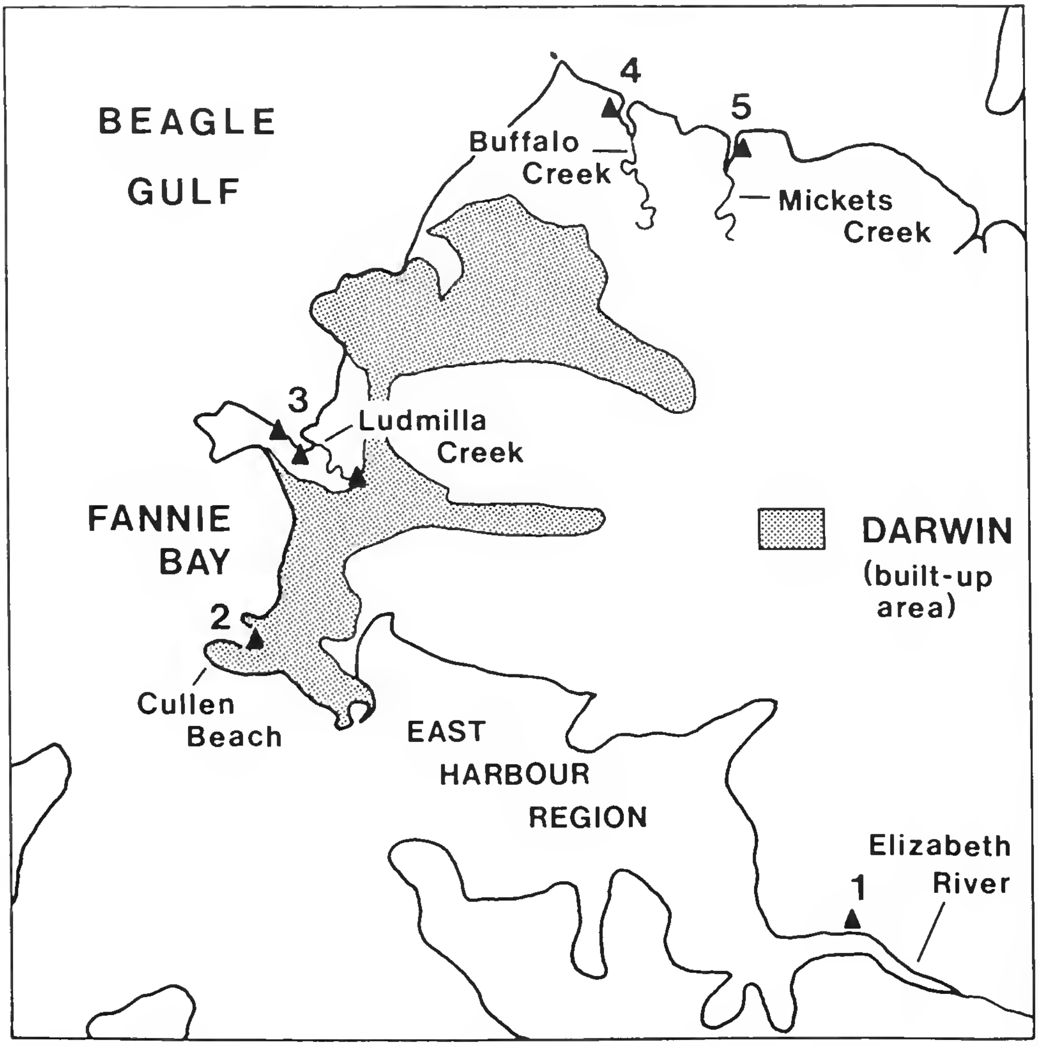

Fig. 1. Study localities in and around Darwin visited in July 1986. See text for explanation of numbers.

The following explanatory list of these abbreviations is supplemented by figures indicating the carapace width of the largest specimens known from Australia (source: George and Jones 1982), which may provide the reader with an impression of the animals' relative sizes.

Abbreviations referring to species from Darwin:

cp	*U. capricornis*	32.3
dp	*U. dampieri*	26.1
el	*U. elegans*	26.6
fl	*U. flammula*	39.6
hs	*U. hirsutimanus*	18.6
mb	*U. mjoebergi*	16.4
pl	*U. polita*	26.2
sg	*U. signata*	20.0
ss	*U. seismella*	17.7

Abbreviations for species from Queensland (used for comparison):

cc	*U. coarctata*	37.4
ds	*U. dussumieri*	39.9
vm	*U. vomeris*	29.2

Main localities of study (i.e. localities that were especially suitable for the study of each *Uca* species) are listed below. These localities (Fig. 1) were visited from 12 to 29 July 1986, and they are briefly described in the following synopsis. The synopsis also provides a full list of *Uca* species in the order of frequency for each locality (for abbreviations of species names see above).

1. Elizabeth River and Creek H, East Harbour Region - river banks shaded by or covered with mangroves: *fl, cp, hs, ss*; near boat ramp: *fl, cp, ss, hs, sg*.

2. Cullen Beach - open stony and muddy sand flats: *ss, mb*; near or among mangroves: *cp, ss, pl*.
3. Ludmilla Creek - Upper Ludmilla Creek, near Dick Ward Drive - among mangroves: *fl, sg, hs, cp, dp*; open loamy salt flats between mangroves and drive: *el*.
   Ludmilla Creek Marina - mangrove clearing around marina: *pl, ss, dp, mb, hs*; open muddy sand flats of the creek's island: *pl, dp, ss*; steep shoulders of creek banks, near and among mangroves: *fl, cp, ss, hs, dp*.
   Mouth of Ludmilla Creek - loamy salt flats with scattered mangrove bushes: *el, mb*.
4. Buffalo Creek - open creek banks near boat ramp: *dp, mb, pl, ss*.
5. Mickets Creek - open creek banks near boat ramp: *hs, fl, pl*; among mangroves: *sg*; open loamy salt flats: *el*.

The fiddler crab fauna of the extensive mangrove creeks of the Harbour Region is relatively depauperate (consisting mainly of *fl, cp, hs, ss*, see locality 1), whereas in the more disturbed urban region, which may offer a variety of different soil types, seven to nine species may occur within relatively short distances (see locality 3).

Key to the *Uca* species of Darwin.

Males.

1. Front (tongue-like interorbital region) broad; pleonal clasping apparatus (hooking rim of thoracic cavity lodging telson) present........*mjoebergi*
   Front narrow; pleonal clasping apparatus absent..............................2

2(1). Outer major dactyl without median groove; outer palm of major chela, at base of pollex, with a large marked triangular depression, often filled with patches of tomentum (pile, woolly hair) ....*dampieri*
   Outer major dactyl with one or two long grooves, the median one always present; no large triangular depression at pollex base..................................3

3(2). Outer major dactyl with two long grooves running most of its length.....4
   Only one long (median) groove present on outer major dactyl......................5

4(3). Gonopod distally tapered, with long tubular projection; gape of minor chela with dense, long setae in distal half. Major chela and merus of walking legs slender................................*elegans*
   Gonopod distally rounded, without long tubular projection; gape of minor chela with a few bristles only; major chela and merus of walking legs broad ....*capricornis*

5(3). Dorsolateral margin of carapace replaced by a row of widely spaced, blunt tubercles or small groups of tubercles ....*seismella*
   Dorsolateral margin of carapace normal, i.e. a continuous, microscopically beaded line.......................................6

6(5). Long groove of outer major pollex lacking or extremely indistinct; distal tubular projection of gonopod directed sternally..................................*polita*
   Long supramarginal groove of major pollex present; distal tubular projection of gonopod directed laterally or sternolaterally..7

7(6). Supramarginal groove of outer major pollex strongly curving upwards towards centre of pollex base, thus not continuous with supramarginal groove of palm; orbital floor usually without a row of accessory granules behind suborbital crenellations.........*flammula*
   Supramarginal groove of outer major pollex everywhere very close to ventral margin, thus fully or nearly continuous with supramarginal groove of palm; orbital floor always with a row of accessory granules behind suborbital crenellations.......................................8

8(7). Gape of minor chela with a pair of enlarged teeth; major chela frequently with patches of tomentum at least in and around supramarginal groove; distal tubular projection of gonopod directed laterally...........*hirsutimanus*
   Gape of minor chela without a pair of enlarged teeth; major chela without tomentum in and around supramarginal groove; distal tubular projection of gonopod directed sterno-laterally....... ....*signata*

Females.

1. Front broad........................*mjoebergi*
   Front narrow 2

2(1). Crenellations of suborbital margin distinct throughout, only a few of them fused in pairs; minor chela widely gaping, gape without serrations......... ....*dampieri*

At least some suborbital crenellations (usually inner ones) fused to form a continuous border...........................3

3(2). Minor chela unusually broad and heavy, prehensile edges with a series of strong triangular teeth, which already start in proximal corner of gape (though highest teeth are located in distal half).....................................4
Minor chela slender (of normal appearance); distinct triangular teeth absent from proximal quarter of gape or totally lacking.............................6

4(3). Dorsolateral margin of carapace disintegrated into a row of widely spaced, blunt tubercles; carpus, propodus and sometimes merus of last walking leg with a patch of tomentum posteriorly... ....*seismella*
Dorsolateral margin of carapace normal, i.e. a continuous, microscopically beaded line; last walking leg without tomentum.....................................5

5(4). Orbital floor with a row of accessory granules behind suborbital crenellations..................*hirsutimanus*
No accessory granules on orbital floor behind suborbital crenellations.......... ....*polita*

6(3) Merus of last walking leg slender (nearly two and a half times as long as broad)...7
Merus of last walking leg broad (about twice as long as broad)....................8

7(6). Orbital floor without a row of accessory granules behind suborbital crenellations; gape of minor chela with a series of long setae in distal half...... ....*elegans*
Orbital floor with a row of accessory granules behind suborbital crenellations; setae in gape of minor chela less conspicuous..........................*signata*

8(6). Gonopore with a large protruding tubercle.............................*flammula*
Gonopore without a large protruding tubercle..........................*capricornis*

SYSTEMATICS

Uca capricornis Crane
(Figs 2 cp, 4 cp)

Uca (Deltuca) dussumieri capricornis Crane, 1975:36 (type locality Broome, W.A.).

Uca capricornis – George and Jones 1982:18 (not material from Hitchinbrook Island, Qld.).

Uca pavo George and Jones, 1982:25 (type locality Broome).

Uca dussumieri – George and Jones 1982:31 (part: material from Darwin and Cape Don, Cobourg Peninsula, N.T.).

Material. NORTHERN TERRITORY: Cape Don, Cobourg Peninsula, 1965, AM P16623, 1 male (21.3 mm); Darwin, 1914, QM W3015, part: cf. *U. flammula*, 7 male (13.0 - 23.9 mm), 1 female (18.5 mm), 1978, ex WAM 119-78, 2 male (11.2 - 12.6 mm), 1986, ZCMU 511, 42 male (6.0 - 27.6 mm), 27 female (6.9 - 24.6 mm). WESTERN AUSTRALIA: Broome, 1963, USNM 137675, holotype of *U. dussumieri capricornis*, 1 male (24.0 mm), 1978, WAM 189-78, holotype of *U. pavo*, 1 male (25.6 mm).

Comparative material of *U. dussumieri* (H. Milne Edwards). QUEENSLAND: Cairns, 1961, QM W2503, 2 male (29.9 - 32.9 mm); Townsville, 1962, QM W3003, 1 male (34.1 mm), 1 female (34.5 mm). INDONESIA: Kuta (Bali), 1983, ZCMU 351, 16 male (16.1 - 21.7 mm), 5 female (7.3 - 21.3 mm).

Comparative material of *U. coarctata* (H. Milne Edwards). QUEENSLAND: Hinchinbrook Island, 1981, WAM 102-81, 5 male (7.0 - 13.5 mm), 2 female (14.6 - 16.3 mm).

Distribution. Northwest and north Australia.

Main localities of study. Ludmilla Creek Marina, Elizabeth River.

Remarks. Apparently, previous confusion concerning *U. capricornis* may have arisen as a consequence of the wide variety of colours of this species and its dramatic ontogenetic colour change (Fig. 2 cp_{1-3}).

U. capricornis passes a juvenile stage of brilliant blue (Fig. 2 cp_1) that may temporarily brighten to a pale blue or white of carapace and walking legs, the eyestalks always being yellow and the male's major cheliped pale yellow to light brown. The second colour stage (Fig. 2 cp_2) is an intermediate one, where the blue colour gradually turns bluish black or black, while some light spots remain on the carapace as well as on the walking legs. These spots are whitish blue or whitish in the male and female, though the latter usually displays yellow patches in addition (in the upper carapace regions). The eyestalks be-

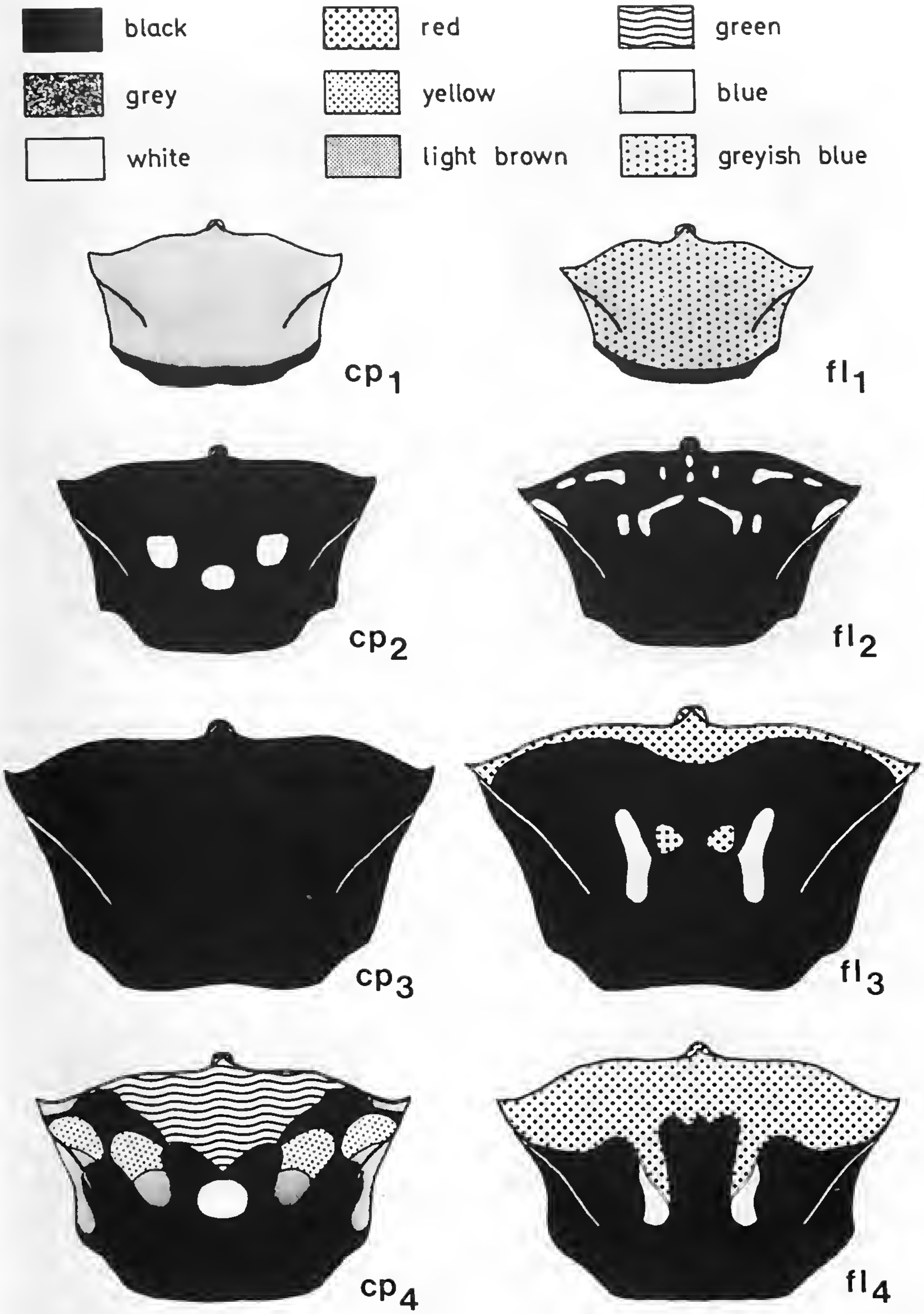

Fig. 2. Typical colour pattern of carapaces in live *Uca* individuals from Darwin (cp_1, cp_2, fl_1, fl_2, juvenile male; cp_3, fl_3, adult male; cp_4, fl_4, adult female). Explanation of abbreviations given in text. Scale line (at bottom of Fig. 3) 10 mm.

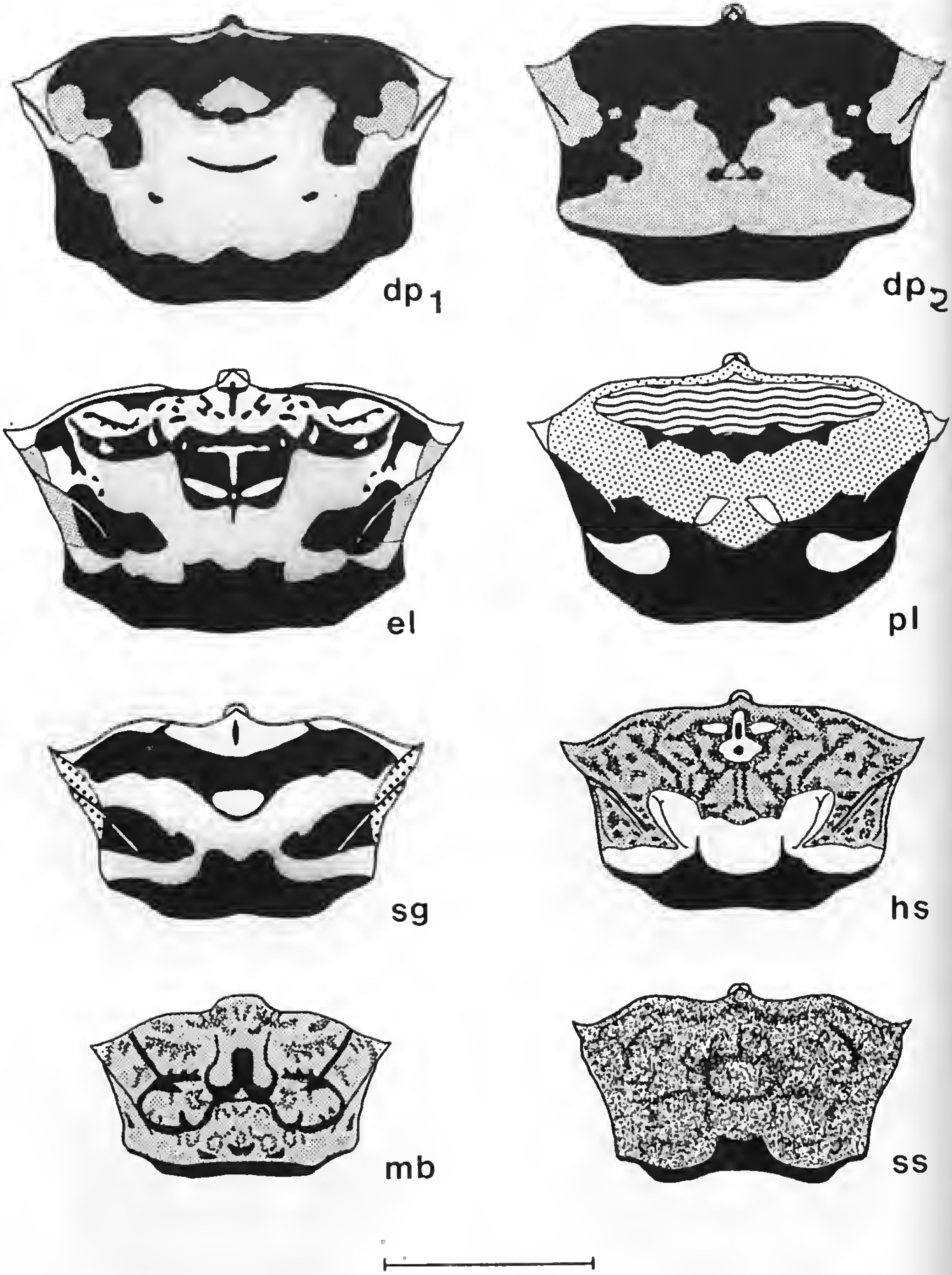

Fig. 3. Typical colour pattern of carapaces in live *Uca* individuals from Darwin (all adult male). Explanation of abbreviations given in text. Scale line 10 mm. Colour key as in Fig. 2.

come greyish green. The major cheliped turns, at least partly, orange or brownish.

The description of *U. capricornis* in George and Jones (1982) mainly refers to small males of the first two colour stages. However, the colour photo of a live *U. capricornis* (*sensu* George and Jones 1982: Fig. 55a) most probably represents a young specimen of *U. flammula* (see this species), because a male *U. capricornis* of this small size would still show yellow eyestalks and blue colours with less grey.

In the third or adult stage ("*pavo*-appearance") the carapace of both sexes may be male-like blackish (Fig. 2 cp_3) with a few occasional lighter spots. Normally, however, there is a striking sexual dimorphism, as the female (Fig. 2 cp_4) retains and refines much of the second colour stage. Most conspicuous is a triangular "scarf-like" field (yellow or green) near the upper margin of the carapace. The sexes frequently have in common a bluish or whitish spot at least on the posterior merus of the fourth walking leg - the last shared remains of their juvenile overall blue colour and the reason for the now-invalid name *U. pavo* (peacock). Perhaps this junior synonym of *U. capricornis* would not have been created, had not Crane (1975:33) explicitly denied this spot for all mature males.

The fact that older material from Darwin and Cobourg Peninsula (see above), previously identified as *U. dussumieri*, now proves to be *U. capricornis* by the shape of its gonopod (Fig. 4 cp_4) revives the idea of allopatry of the two forms: *U. capricornis* as the Dampierian and *U. dussumieri* as the Solanderian species. Further weight to this idea is added by the result that "*U. capricornis*" from Queensland (*sensu* George and Jones 1982:21) is *U. coarctata* in reality (see comparative material).

Uca flammula Crane
(Figs 2 fl, 4 fl)

Uca (Deltuca) coarctata flammula Crane, 1975:56 (type locality Darwin, N.T.).

U. flammula – George and Jones 1982:40.

Uca coarctata – George and Jones 1982:37 (part: material from Darwin, N.T.).

Material. NORTHERN TERRITORY: Darwin, 1914, QM W3015, part: cf. *U. capricornis*, 2 male (22.1 - 24.9 mm), 1978, ex WAM 105-78, 1 male (15.8 mm), 1978, ex WAM 107-78, 1 male (15.6 mm), 1986, ZCMU 512, 55 male (7.4 - 31.4 mm), 36 female (11.1 - 25.7 mm).

Comparative material of *U. coarctata* (H. Milne Edwards). QUEENSLAND: Brisbane River, 1986, ZCMU 5110, 10 male (15.9 - 27.8 mm), 6 female (14.1 - 21.6 mm).

Distribution. Northwest and north Australia, according to Crane (1975) also parts of west New Guinea.

Main localities of study. Upper Ludmilla Creek, Ludmilla Creek Marina, Elizabeth River.

Remarks. This most conspicuous and biggest of all Darwin fiddler crabs is subject to an ontogenetic colour change that is not less dramatic than the one in *U. capricornis*. Unfortunately, Crane (1975:54) mentions with respect to both subspecies of *U. coarctata* (i.e. including *flammula*) that "males, females, and immature crabs are similarly colored".

Juvenile crabs (Fig. 2 fl_1) appear uniform light greyish blue, except for the darker eyestalks and the male's pale yellow major cheliped. As these males have no trace of red colour and are already very active in waving display they can easily be mistaken for a species of their own. On the other hand, they can be confused with juvenile *U. capricornis*. These, however, have yellow eyestalks instead of dark blue ones.

During an intermediate colour stage (Fig. 2 fl_2) the carapace turns black (at least the posterior regions) at first being mottled with a variety of lighter marks, which are usually of more irregular shape than in *U. capricornis*. All appendages gradually become brownish to orange with the male's major cheliped being in advance.

At the final stage (Fig. 2 fl_3) the appendages (except for the major dactyl of the male) and all underparts of the crab have become bright orange red to scarlet. This colour extends to the orbits and eyestalks and to the anterior eighth (male) to quarter (female) of the otherwise black carapace. The black region can still be interrupted by brighter spots. Typically there are at least two comma-like vertical marks (white or red or a combination as depicted for the female, Fig. 2 fl_4).

Because of their characteristic colour pattern, living individuals of *U. flammula* are easily separated from *U. coarctata* (which look more like U. capricornis). However, the

identification of isolated preserved specimens can be a very difficult task. The male gonopods of the two species are very similar (Fig. 4 fl, cc) and thus not reliable. The subdistal tooth of the major dactyl (large and hook-like in *U. coarctata* only, Crane 1975) is not yet present in young males and a distinct row of granules on the orbital floor (thought to be diagnostic for *U. coarctata*) can also be present in *U. flammula*: it was found in one male out of 55 and seven females out of 36 within the *flammula*-like coloured Darwin material collected in 1986. In addition, six males and no less than 12 females have at least a few orbital granules.

As the Darwin specimens of "*U. coarctata*" of 1978 (*sensu* George and Jones 1982:40) were identified from preserved, mainly immature material, on the base of the accessory granules these specimens cannot serve as a proof for the presence of the species in Darwin. Though we were not able to re-examine the material from Goomadeer River (George and Jones 1982:40), we return to the assumption that *U. coarctata* is a Solanderian species, which does not occur in northwest and north Australia.

Uca dampieri Crane
(Figs 3 dp, 5 dp)

Uca (Thalassuca) vocans dampieri Crane, 1975:91 (type locality Broome, W.A., Crane 1975:597, not Darwin as indicated by Crane 1975:89).

Uca dampieri – George and Jones 1982:67.

Uca vomeris – George and Jones 1982:70 (part: material from Darwin).

Material. NORTHERN TERRITORY: Darwin, 1978, ex WAM 146–78, 2 male (16.2 – 19.8 mm), 1978, ex WAM 274–79, 2 male (14.4 – 15.0 mm), 1 female (17.2 mm), 1986, ZCMU 513, 36 male (7.4 – 24.0 mm), 17 female (12.2 – 20.5 mm). WESTERN AUSTRALIA: Broome, 1963, USNM 137671, holotype of *U. vocans dampieri*, 1 male (19.0 mm).

Comparative material of *U. vomeris* McNeill. QUEENSLAND: Sabai Island, Torres Strait, AM P31745, P31758, 17 male (10.0 – 21.3 mm), 13 female (13.4 – 19.5 mm); Yam Island, Torres Strait, 1976, AM P31747, P31759, P31760, P31995, 21 male (9.2 – 22.1 mm), 12 female (9.0 – 17.2 mm); Shorncliffe, 1986, ZCMU 5111, 6 male (11.5 – 21.0 mm), 3 female (8.8 – 15.3 mm); Brisbane, 1981, WAM 120–81, 4 male (23.1 – 29.2 mm), 1 female (21.5 mm).

Distribution. Northwest and north Australia.

Main localities of study. Ludmilla Creek Marina, Buffalo Creek.

Remarks. The male gonopod of *U. dampieri* (Fig. 5 dp) is very dissimilar to that of the closely related *U. vomeris* (Fig. 5 vm) the latter gonopod being strongly twisted anticlockwise and having the palp (thumb) in a distal instead of a subdistal position (Crane 1975). Any attempts to find other reliable morphological characters for separating the two species (Crane 1975; George and Jones 1982) have failed until now - apparently, because of the variability of the two forms, particularly of *U. dampieri*.

The carapace of *U. dampieri* is greyish brown in juveniles. In adults, it can be either mostly blue (Fig. 3 dp_1) or mostly light brown to cream (Fig. 3 dp_2) with various combinations of the two colours and black or dark grey patterns in addition. In the course of colour brightening during low tide, most of the animal, except for the chelae and walking legs, may turn white. This is not confined to males, but also occurs in females (cf. a similar brightening of colours in females of the related eastern Pacific *U. stylifera*, von Hagen 1968:444-445).

The shape of the major cheliped of the male is, likewise, subject to a strong variation, especially with respect to the subdistal triangular projection on the upper margin of the pollex. This tooth can be small (as in the holotype) or even absent in *U. dampieri*, but it can be huge as well.

When relying on the shape of the gonopod only, all alleged *U. vomeris* from Darwin turn out to belong to *U. dampieri*. Though we were unable to re-examine the material from Liverpool River (George and Jones 1982:73), we conclude that *U. vomeris* is absent from northwest Australia (as was generally thought prior to the publication of George and Jones 1982). Its presence is, however, confirmed for the islands of Torres Strait mentioned above (see comparative material).

Uca elegans George and Jones
(Figs 3 el, 5 el)

Uca elegans George and Jones, 1982:22 (type locality Derby, W.A.).

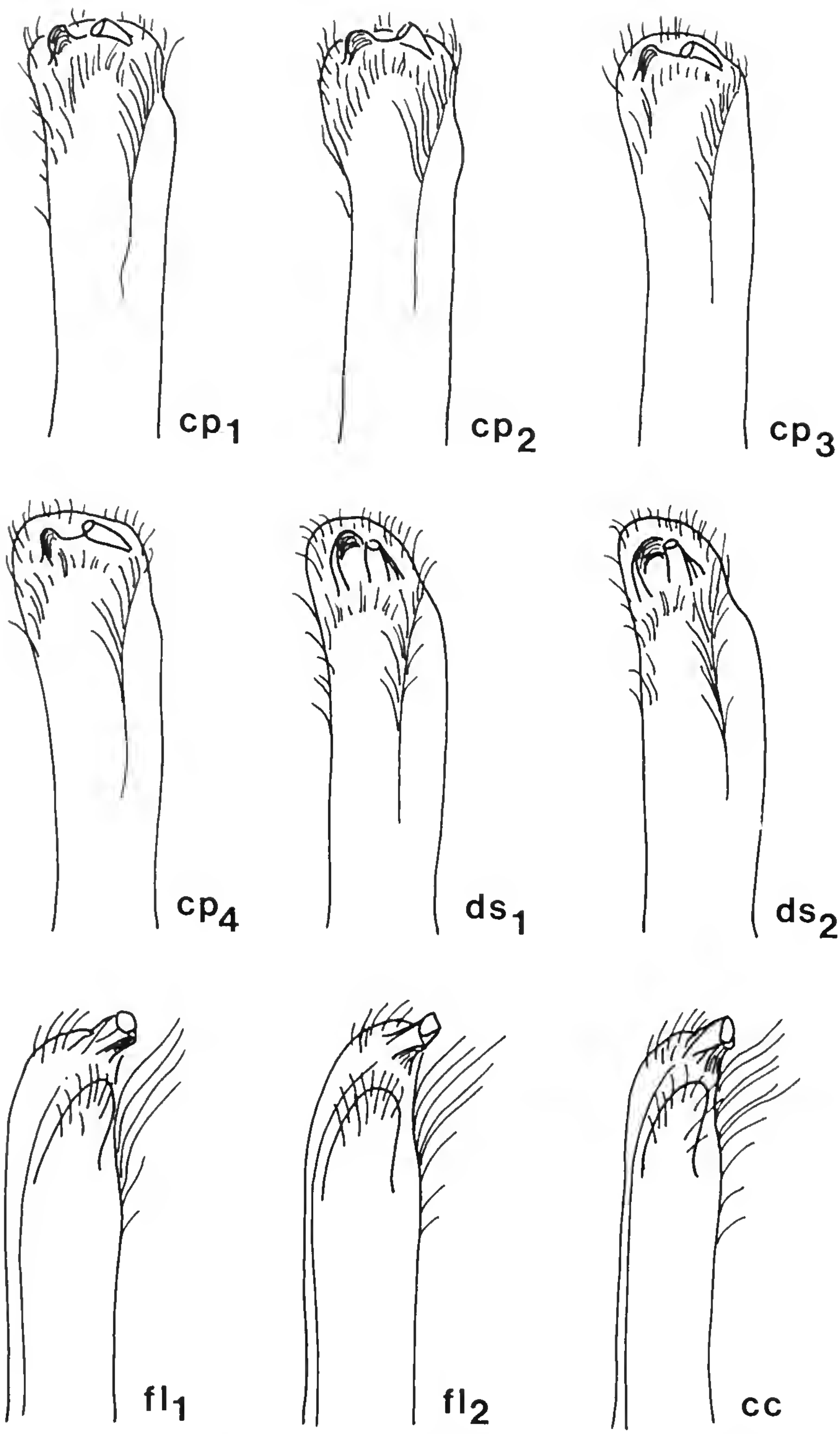

Fig. 4. Terminal portions of male right gonopods (first pleopods) in lateral (outer) view (drawings at top and centre) and sternal (anterior) view (at bottom), respectively. Explanation of abbreviations given in text. Figures (in mm) refer to carapace width. cc 22.2 (Brisbane River 1986); cp_1 23.0 (Darwin 1986, typical "*pavo-appearance*"); cp_2 24.0 (holotype); cp_3 12.6 (Darwin 1978); cp_4 20.9 (Darwin 1914, alleged *U. dussumieri*); ds_1 29.9 (Cairns 1961); ds_2 21.6 (Kuta, Bali 1983); fl_1 19.0 (Darwin 1986); fl_2 15.6 (Darwin 1978, alleged *U. coarctata*).

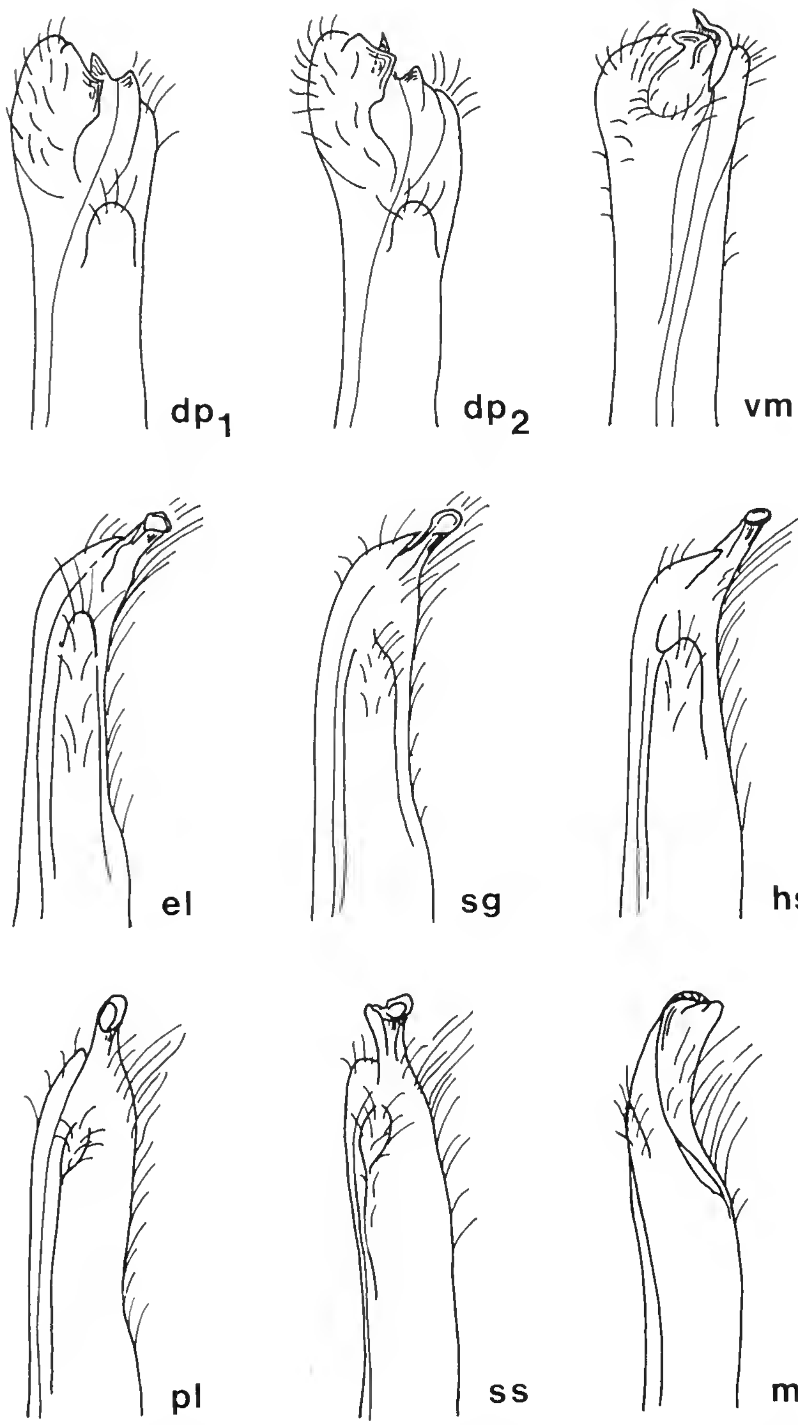

Fig. 5. Terminal portions of male right gonopods in sternal (anterior) view. Explanation of abbreviations given in text. Figures (in mm) refer to carapace width. dp_1 19.8 (Darwin 1978, alleged *U. vomeris*); dp_2 18.9 (holotype); el – ss (Darwin 1986): el 22.0; hs 17.0; mb 14.9; pl 21.3; sg 17.1; ss 17.2; vm 19.6 (Shorncliffe, Qld. 1986).

Material. NORTHERN TERRITORY: Darwin, 1986, ZCMU 514, 75 male (10.3 – 24.8 mm), 33 female (10.2 – 20.0 mm).

Comparative material of *U. australiae* Crane. WESTERN AUSTRALIA: Broome, 1911, USNM 64250, holotype of *U. demani australiae*, 1 male (about 25.0 mm).

Distribution. Northwest and north Australia.

Main localities of study. Upper Ludmilla Creek, mouth of Ludmilla Creek, Mickets Creek.

Remarks. Judged from the colour pattern of the carapace (Fig. 3 el, cf. with sg), from the waving display (von Hagen, in prep.) and from several morphological characters (including the shape of the gonopod, Fig. 5 el, cf. with sg and hs), *U. elegans* is close to *U. signata* and *U. hirsutimanus* and not a member of the *dussumieri-capricornis* assemblage as was, in view of the two dactyl grooves, originally assumed by George and Jones (1982).

U. elegans was compared with the single male (holotype) that exists of *U. australiae* (from Broome, collected by E. Mjöberg in 1911), because in both taxa the gape of the minor cheliped is provided with a conspicuous series of setae distally. For the rest, however, *U. australiae* is unlike *U. elegans*, especially in the shape of its gonopod.

Uca signata (Hess)
(Figs 3 sg, 5 sg)

Gelasimus signatus Hess, 1865:146 (type locality Australia).

Uca (Australuca) bellator signata – Crane 1975:67.

Uca (Australuca) bellator minima Crane, 1975:68 (type locality Darwin; regarded as a synonym of *U. signata* already by George and Jones 1982:44).

Uca signata - George and Jones 1982:44.

Material. NORTHERN TERRITORY: Darwin, 1956, USNM 137668, holotype of *U. bellator minima*, 1 male (10.0 mm); 1986, ZCMU 515, 78 male (7.9 – 17.7 mm), 42 female (7.9 – 14.7 mm).

Distribution. From northwest to northeast Australia.

Main localities of study. Upper Ludmilla Creek, Mickets Creek.

Remarks. George and Jones (1982) are correct in concluding that Crane's specimens of *U. bellator minima* are juveniles of *U. signata*. At least one of the other juveniles they used for comparison came from Townsville (George and Jones 1982: Tab. 4) so that *U. minima* was compared also with *U. signata* from the east coast of Australia. However, the problem of possible differences between eastern and northwestern populations of *U. signata* has never been made an explicit research topic of its own. In case essential differences of behaviour or colour will be found in future, one might make use of Crane's subspecific name *minima* for the Dampierian populations.

Uca hirsutimanus George and Jones
(Figs 3 hs, 5 hs)

Uca hirsutimanus George and Jones, 1982:49 (type locality Derby, W.A.).

Material. NORTHERN TERRITORY: Darwin, 1986, ZCMU 516, 36 male (8.3 - 18.0 mm), 30 female (8.9 - 16.1 mm).

Distribution. Northwest and north Australia, Torres Strait.

Main localities of study. Mickets Creek, Elizabeth River, Ludmilla Creek.

Remarks. Except for the colour (Fig. 3 hs), *U. hirsutimanus* is very much like *U. signata*. The two species live sympatrically west of Cape York only. Interspecific differences were listed by George and Jones (1982: Tab. 5). A supplementary character is the different inclination of the terminal tube of the male gonopod (see key and Fig. 5 hs).

Uca polita Crane
(Figs 3 pl, 5 pl)

Uca (Australuca) polita Crane, 1975:72 (type locality Gladstone, Qld.).

Uca polita – George and Jones 1982:60.

Material. NORTHERN TERRITORY: Darwin, 1986, ZCMU 517, 51 male (9.8 – 23.4 mm), 14 female (13.0 – 21.0 mm). QUEENSLAND: Shorncliffe, 1986, ZCMU 5112, 1 male (16.1 mm).

Comparative material of *U. longidigitum* (Kingsley). QUEENSLAND: Brisbane River, 1986, ZCMU 5113, 26 male (8.1 – 19.5 mm), 8 female (7.5 – 14.2 mm).

Distribution. From northwest to northeast Australia.

Main locality of study. Ludmilla Creek Marina.

Remarks. Most characteristic of the colour pattern of *U. polita* are the two large white or cream eye-like spots of the posterior carapace and the frequent occurrence of greenish colours in the anterior carapace regions (Fig. 3 pl). Related colours and patterns can be found in large specimens of the eastern form *U. longidigitum;* (the nomenclatural change to "*longidigita*" by Crane 1975 is an incorrect subsequent spelling. because *longidigitum* is not an adjective). This fact and the common loss of distinct grooves on outer pollex and palm of the major cheliped indicate a close relationship between the two species. The treatment of *U. longidigitum*, like *U. signata*, as a subspecies of *U. bellator* (see Crane 1975) is misleading.

Uca seismella Crane
(Figs 3 ss, 5 ss)

Uca (Australuca) seismella Crane, 1975:70 (type locality Darwin, N.T.).

Uca seismella – George and Jones 1982:56.

Material. NORTHERN TERRITORY: Darwin, 1986, ZCMU 518, 37 male (3.4 – 17.2 mm), 18 female (5.7 – 12.4 mm).

Distribution. From northwest to northeast Australia.

Main localities of study. Ludmilla Creek Marina, Cullen Beach.

Remarks. This is the smallest and most fragile of Australian narrow fronts. It is also the most cryptic (Fig. 3 ss), although its display is extremely conspicuous. This display was filmed not only in Darwin but also on the banks of the Brisbane River, close to the Botanical Gardens of Brisbane City in August, 1986. Although the crab itself was not collected, this cinematographic sample confirms the extension of the species' geographic range: the previous southermost record was the Mary River (George and Jones 1982).

In the material from Darwin the terminal tube of the male gonopod (Fig. 5 ss) is provided with a definite flexible mesial keel, which is not mentioned by previous authors.

Uca mjoebergi Rathbun
(Figs 3 mb, 5 mb)

Uca mjöbergi Rathbun, 1924:9 (type locality Broome, W.A.).

Uca (Celuca) lactea mjobergi – Crane 1975:299.

Uca mjobergi – George and Jones 1982:80.

Material. NORTHERN TERRITORY: Darwin, 1986, ZCMU 519, 39 male (5.4 – 15.0 mm), 37 female (7.7 – 11.7 mm).

Distribution. Northwest and north Australia, according to Crane (1975) also northwest New Guinea.

Main localities of study. Mouth of Ludmilla Creek, Ludmilla Creek Marina, Buffalo Creek.

Remarks. This is the only broad-fronted species that occurs in Darwin (*U. triangularis* is known from Melville Island only, George and Jones 1982). Both the brownish marbled carapace (Fig. 3 mb) and the canary yellow cheliped may be considered cryptic, the former imitating sand, the latter yellow mangrove leaves (cf. a similar colour correspondence in the neotropical *U. thayeri*, von Hagen 1978).

The spelling "*mjobergi*" (Crane 1975) is not in conformity with the International Code of Zoological Nomenclature (1985, Art. 32) and should be replaced by the spelling mjoebergi.

DISCUSSION

The studies of Crane (1975), George and Jones (1982) and the corrections mentioned in the present paper provide the following zoogeographic assumptions:

1. There are 16 species of *Uca* confirmed for the Australian fauna; *U. australiae* Crane and *U. crassipes* (Adams and White)[1] should be omitted until further specimens have been discovered (George and Jones 1982). Although the exact boundaries are not yet known for each species, it seems warranted to suppose that 12 of the 16 species are strictly or mainly confined to one of the two northern biogeographic provinces (Dampierian and Solanderian *sensu* Hedley 1904) as indicated in Table 1, section I. Of these 12 species, six are members of the Dampierian province (northwest and north coasts, west of Torres Strait), six others seem to be confined (now again cf. George and Jones 1982) to the northeast coasts, the Solanderian province, with *U. perplexa* and *U. vomeris* occurring also south of Queensland. Only four species (Tab. 1, section II) are bilat-

1. Note added in proof: *U. crassipes* has since been discovered in Cairns (von Hagen, in prep.)

Table 1. Occurrence of the 16 confirmed Australian species of *Uca* in the two tropical zoogeographic provinces.

		Dampierian province	Solanderian province
I.	Species occurring in one province		
	a) Species forming pairs	*U. capricornis*	*U. dussumieri*
		U. flammula	*U. coarctata*
		U. dampieri	*U. vomeris*
		U. mjoebergi	*U. perplexa*
	b) Species not forming pairs	*U. elegans*	
		U. hirsutimanus	
			U. longidigitum
			U. tetragonon
II.	Species occurring in both provinces	*U. polita*	
		U. seismella	
		U. signata	
		U. triangularis	

eral, i.e. members of both provinces ("circum-tropical" *sensu* Davie 1985).

2. Eight of the 16 species mentioned are endemic to Australia (*U. capricornis, U. dampieri, U. elegans, U. hirsutimanus, U. longidigitum, U. polita, U. seismella, U. signata*) and three others are endemic at least to Australasia (*U. flammula, U. mjoebergi, U. vomeris*, see Crane 1975). Six of these 11 endemic species occur only in the Dampierian province. This fact gave rise to the idea "that northwestern Australia has been a major region of speciation for the genus *Uca* and this region has been efficiently isolated from the east coast" (Davie 1985: 263-264).
3. Four of the Darwin species that now appear to be Dampierian endemics have closely related eastern counterparts. The species pairs resulting are illustrated in section I a of Table 1. All these pairs seem to occur in an allopatric pattern of distribution, presumably separated by the Torres Strait region. However, to give these forms only subspecific rank (as Crane 1975 did) would be unwise for the following practical reasons: (a) There might exist at least small zones of overlap, not yet known, within the Cape York region. (b) Even without any local overlap it holds true that all these forms are well defined by different morphological characters including different colour patterns. In the future there may be an urgent need to use the subspecific rank in order to distinguish between less well-defined local forms within some of the eight species mentioned, i.e. within a certain Australian province or within the vast range of the three non-endemic partners *U. coarctata, U. dussumieri* and *U. perplexa*. Use of the subspecific rank may also be desirable when more essential differences are found between western and eastern populations of the bilateral species (Tab. 1, section II). Any differences found within these species are predicted to be of less weight than those within the pairs of species mentioned in Table 1, section Ia.

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OFFSHORE FISHES OF THE ARAFURA SEA

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ABSTRACT

The species composition, zoogeographic affinities and importance to fisheries of the offshore fish fauna of the Arafura Sea is examined. A total of 527 species from 141 families are recorded. Most of the fishes are shallow-water, benthic species belonging to widespread Indo-Pacific families. Remaining fishes are deeper water or epipelagic forms with Indo-Pacific or Cosmopolitan distributions. The 10 most speciose families (Carangidae, Lutjanidae, Carcharhinidae, Leiognathidae, Nemipteridae, Platycephalidae, Serranidae, Scorpaenidae, Mullidae, Bothidae) contain about 34% of the total number of species. Greatest faunal affinity is seen with the fish fauna of the North-west Shelf of Western Australia. Fishing methods in the Arafura Sea include bottom trawl, gillnet, longline, and handline. Of the total species recorded, 491 (93.2%) were taken by bottom trawl; 108 species (20.5%) are retained as catch; and 163 by-catch species (30.9%), presently discarded, are potentially useful for food, bait, or processing as fish meal and petfood. Some 23 species (4.4%) are dominant in bottom trawls and comprise about 70% of the total catch biomass.

KEYWORDS: Offshore fish fauna, Arafura Sea, taxonomic composition, zoogeography, fisheries importance.

INTRODUCTION

The fishes of the Arafura Sea are probably the least well known of any Australian region. Much of our present knowledge of the fish fauna of northern Australia is based on scattered records and collections of fishes mainly from shallow water and inshore reef areas (e.g. Paradice and Whitley 1927; Taylor 1964). Despite the fact that since 1971 the Arafura Sea has supported an important foreign trawl and gillnet fishery, there have been few collections from offshore fishing vessels until comparatively recently.

In this paper we examine the species composition and zoogeographic affinities of the offshore fish fauna of the Arafura Sea. Our work is based mainly on trawl and other offshore collections made over the last 10 years, but also includes earlier records. It is to be hoped that this paper will provide a taxonomically up-to-date and useful reference to the commercially important and common fishes taken in demersal trawls or gillnets, as well as the lesser known species which form much of the by-catch of these fisheries.

STUDY AREA

The present work deals with fishes collected from offshore localities of the Arafura Sea, generally from that part of the shelf beyond 12 nautical miles (22 km) from the coast, outside of the restricted area of the Australian Fishing Zone. These offshore waters of the Arafura Sea are fished mainly by foreign vessels operating under bilateral or joint-venture arrangements (Branford 1984).

The Arafura Sea (Fig. 1) covers an area of about 650,000 km^2. This area, which includes the Aru Islands and deep Aru Trough, is bordered on the north by the Outer Banda Arc and coast of Irian Jaya; on the east by Torres Strait (141°E); on the south by the Gulf of Carpentaria (here defined as extending southwards of a line from Cape Arnhem to Crab I.,

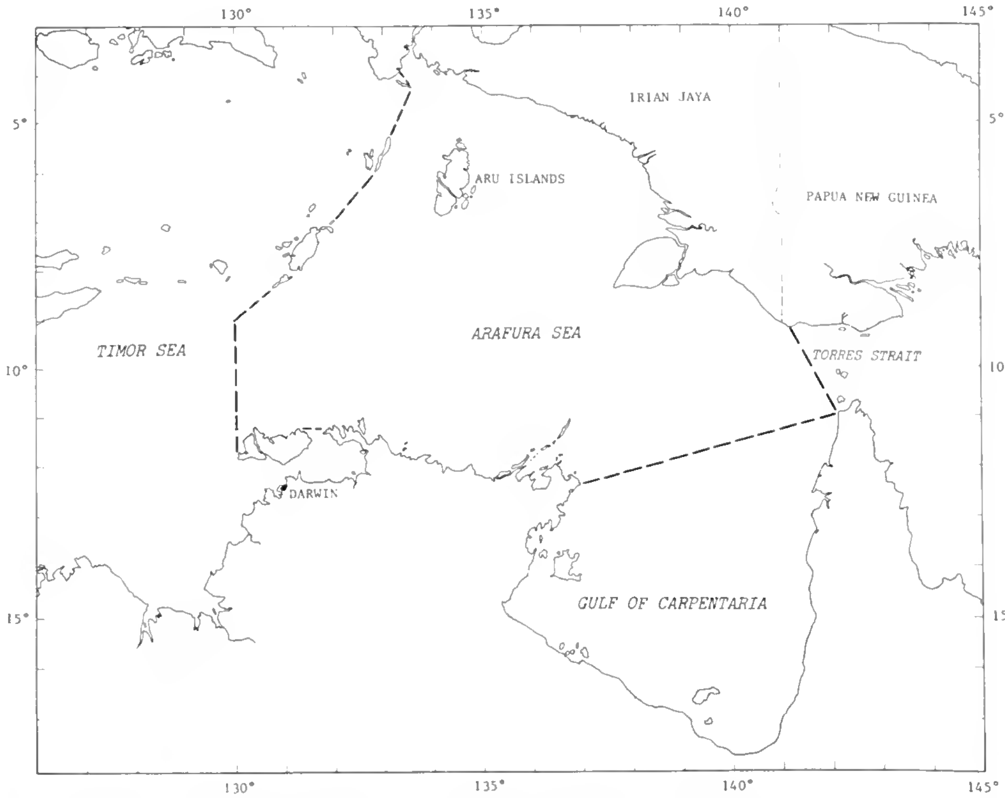

Fig. 1. Location map of the Arafura Sea and its boundaries (dashed lines) as defined in the text.

off Cape York Peninsula) and the northern Australia coast; and on the west by the 130°E meridian (Tjia 1966).

The Arafura Sea largely covers a vast, shallow bank (the Arafura Shelf) that is composed mainly of glauconitic sand and calcareous mud (Tjia 1966; Jongsma 1974). Depths over most of the Arafura Shelf generally range between 50-80 m. Deeper parts are located beyond the edge of the continental shelf to the north-west. Here the Arafura Shelf is separated from the outer Banda Arc by the deep Aru Trough (3650 m) which has an area of 1,000 km^2 below the 3,000 m isobath (Tjia 1966).

Tjia (1966) summarised hydrographic conditions in the Arafura Sea. Surface salinities range from 33.6‰ - 35‰ Sea surface temperatures are at a maximum in December-February (28.4°C) and are lowest in June-August (26.1°C). During summer, winds blow from west north-west (north-west monsoon) in the area of the Arafura Sea between 4°-10°S (Beaufort force 1.5-4.4). Off the coast of Australia, the wind direction is north north-west (Beaufort force 1.5-2.4). During winter, the south-east monsoon winds blow with equal strength across the whole Arafura Sea. Surface currents in the Arafura Sea north of 8°S have irregular directions and are generally unsteady. South of this latitude, the currents are predominantly westward running at 10-12 nautical miles per day (n mi/day) during winter. In summer the currents have no general directions; in the south-west and south-east parts of the sea, the currents are directed outward, into the Indian Ocean and the Coral Sea respectively. A current system revolves counterclockwise around 10°S, 136°E. Speeds do not exceed 10 n mi/day. Tidal ranges in the Arafura Sea reach 4.5 m at springs on the coast of Irian Jaya and 2.5 m at Dobo, Aru Islands. Maximum tidal currents off the Irian coast reach 4.6 n mi/day toward the north north-west. Off the Australian coast, tidal currents of 5-10 n mi/day occur (Tjia 1966).

PREVIOUS WORK

The first scientific collections of fishes from the Arafura Sea were made by H.M.S. *Challenger* in September 1874 (Stations 188,

190, 191). In reports on the fishes collected by the *Challenger*, Günther (1878, 1880, 1887, 1889) recorded 40 species from the Arafura Sea, including 13 species which he described as new. Apart from a few scattered records there has been little further contribution to our knowledge of the fish fauna of the Arafura Sea.

Exploratory fishing surveys in the Arafura Sea and Gulf of Carpentaria were carried out by research vessels of the Soviet Union between 1967-70 and up to 300 species recorded (Shuntov 1971). Unfortunately, except for listing some of the more common trawl species (Shuntov 1971), the Soviet records are unpublished and their specimens are unavailable.

Extensive exploratory fishing in northern Australia was also undertaken by Taiwanese vessels during the early 1970's. Wei *et al.* (1972) recorded 111 species from trawls made by the Taiwanese research vessel *Hai Ching* in the Arafura sea from March to May 1972. Specimens of species reported by this survey could not be located and are included herein as unconfirmed records.

The United States research vessel *Alpha Helix* visited the Arafura Sea briefly in March 1975 and made a number of midwater and bottom trawls. Some of the fishes collected from these trawls are in the Australian Museum, and include at least one new species recently described by Castle and Paxton (1984).

Two exploratory trawl surveys of the shelf waters of the Arafura Sea and Gulf of Carpentaria were carried out by the Commonwealth Scientific and Industrial Organisation's (CSIRO) chartered research vessel FRV *Soela* in 1980-81 (Okera and Gunn 1986). These cruises resulted in some 320 species being recorded from the Arafura Sea, excluding the Gulf of Carpentaria (Sainsbury *et al.* 1985).

The present list of species is based primarily on specimens collected during a 3 year study of the by-catch of demersal trawl fish assemblages of the Arafura Sea (Russell and Houston, in prep.). This work, begun in 1985, involved the collection of many thousands of specimens, representative material of which is deposited in the Northern Territory Museum (NTM). Other recent collections of fishes were obtained from prawn trawlers operating in deep shelf waters and on the continental slope north of Bathurst Island and Melville Island. Offshore collections of fishes from the Arafura Sea now include over 650 lots and more than 1500 specimens in the NTM.

METHODS

Species records for offshore fishes of the Arafura Sea are included as a checklist (Appendix 1). The checklist is arranged by family and generally follows the phylogenetic arrangement proposed for elasmobranch fishes by Compagno (1973) and for teleosts by Greenwood *et al.* (1966), except where recent work indicates inclusion (e.g. Synanceiidae in Scorpaenidae) or separation (e.g. Harpadontidae from Synodontidae) of families. Spelling of family names follows emendations suggested by Steyskal (1980). Under each family the species are arranged alphabetically by genus and species, together with the name of the original author.

Unless otherwise indicated, species records are based on specimens in the NTM or field records (indicated by FR) from trawl samples (Russell and Houston, in prep.). Other records are indicated in parentheses following the species citation. Species in the Australian Museum, Sydney, are indicated by AMS; species recorded by Sainsbury *et al.* (1985) are indicated by CSIRO; records by other authors are cited in full and are included in the references. Every effort was made to confirm species identifications and records. For some unidentified species, the 6 digit CSIRO species code used by Sainsbury *et al.* (1985) is included in parentheses following the genus name to assist with future identification. Questionable or unconfirmed records are indicated by a question mark (?) before the record; uncertain identifications are indicated by a question mark following the species citation. Where necessary, nomenclatural or taxonomic remarks are enclosed by square brackets following the family or species record. Annotations to the checklist include method of capture, indication of species taken by Taiwanese and Thai vessels, and indication of species taken by commercial fishing vessels as catch or discards. Because discard practices varied from vessel to vessel, particularly between Taiwanese and Thai vessels, we regarded catch as species that were retained by some or all vessels, and discards as species that were trashed by all vessels.

TAXONOMIC COMPOSITION OF THE FISH FAUNA

The fish fauna of the Arafura Sea includes 527 species from 141 families (Tables 1, 2, Appendix 1). The great majority of fishes (111 families, 481 species) are shallow-water, benthic forms that typically inhabit depths down to about 100m. These shorefish families are distributed widely throughout the tropical Indo-Pacific (Springer 1982). The remaining families are mainly deeper water and epipelagic forms, most of which have widespread Indo-Pacific or cosmopolitan distributions.

A few families dominate the fish fauna of the Arafura Sea (Table 1), and the 10 most speciose families (Carangidae, Lutjanidae, Carcharhinidae, Leiognathidae, Nemipteridae, Platycephalidae, Serranidae, Scorpaenidae, Mullidae, Bothidae) together contain about 34% of the total number of species. Three endemic families (Tetrabrachiidae, Leptobramidae, Rhinoprenidae) are known from northern Australia (Wilson and Allen 1987), and two of these (Tetrabrachiidae, Leptobramidae) are recorded from the Arafura Sea.

Comparison With Other Areas

Family composition. The number of fish families from the Arafura Sea is similar to that of the North-west Shelf, and is greater than the number of families reported for other tropical areas of northern Australia, including coral reef areas (Table 2). In part the high number of families for the Arafura Sea is due to the inclusion of deep water and oceanic families, but even excluding these groups, the number of shorefish families represented in the Arafura Sea (111) is high compared with other areas.

The number of families in other areas that are shared with the Arafura Sea is high (Table 2), largely reflecting common faunal origins. Greatest similarity is seen between the Arafura Sea and the south-eastern Gulf of Carpentaria (92%), Gulf of Papua (85.7%) and the North-west Shelf (82.1%). Similarity in overall family composition is somewhat less for coastal Queensland (72.2%), the southern Great Barrier Reef (71.3%) and Rowley Shoals/Scott Reef (68.8%).

Differences in family composition also are seen in a comparison of the most speciose families from various areas of northern Australia (Table 1). The Arafura Sea and North-west Shelf show greatest similarity in family composition, with 8 of 10 dominant families being the same. However, only 3 of the 10 dominant families in the south-eastern Gulf of Carpentaria, and 4 of the 10 dominant families in Queensland and the Gulf of Papua are dominant also in the Arafura Sea. Differences in family composition are even more marked for the southern Great Barrier Reef and Rowley Shoals/Scott Reef, where only 1 of 10 dominant families is dominant also in the Arafura Sea.

These differences in family composition suggest that the fish fauna of tropical northern

Table 1. Comparison of the composition of the 10 most speciose fish families (and No. species in each family) from the Arafura Sea with the most speciose families from the N. W. Shelf[1], S. Gulf of Carpentaria[2], Gulf of Papua[3], Coastal Queensland[4], S. Great Barrier Reef[5], and Rowley Shoals/Scott Reef[6].

Arafura Sea		N.W. Shelf		S. Gulf of Carpentaria		Gulf of Papua		Coastal Queensland		S. Great Barrier Reef		Rowley Shoals/ Scott Reef	
Carangidae	(38)	Carangidae	(43)	Carangidae	(21)	Carangidae	(29)	Scorpaenidae	(23)	Gobiidae	(104)	Gobiidae	(90)
Lutjanidae	(21)	Serranidae	(28)	Clupeidae	(13)	Scorpaenidae	(17)	Carangidae	(17)	Labridae	(69)	Pomacentridae	(65)
Carcharinidae	(19)	Scorpaenidae	(24)	Scorpaenidae	(12)	Clupeidae	(15)	Bothidae	(16)	Pomacentridae	(69)	Labridae	(59)
Leiognathidae	(16)	Botbidae	(22)	Apogonidae	(12)	Sciaenidae	(14)	Tetraodontidae	(13)	Blenniidae	(40)	Apogonidae	(43)
Nemipteridae	(16)	Carcharhinidae	(21)	Leiognathidae	(12)	Ariidae	(13)	Platycephalidae	(12)	Apogonidae	(33)	Serranidae	(32)
Platycephalidae	(15)	Nemipteridae	(20)	Gobiidae	(12)	Engraulididae	(12)	Apogonidae	(11)	Serranidae	(32)	Chaetodontidae	(29)
Serranidae	(15)	Apogonidae	(19)	Soleidae	(12)	Tetraodontidae	(12)	Callionymidae	(8)	Chaetodontidae	(32)	Blenniidae	(26)
Scorpaenidae	(14)	Playcephalidae	(18)	Ariidae	(11)	Leiognatbidae	(11)	Monacanthidae	(7)	Acanthuridae	(25)	Muraenidae	(23)
Mullidae	(14)	Labridae	(18)	Sciaenidae	(9)	Lutjanidae	(11)	Triacanthoididae	(7)	Muraenidae	(23)	Holocentridae	(22)
Bothidae	(13)	Lutjanidae	(17)	Tetraodontidae	(9)	Apogonidae	(10)	Triglidae	(7)	Scaridae	(22)	Acanthuridae	(21)

[1] Data from Sainsbury *et al.* (1985: pp 328-350, regions A + B).
[2] Data from Rainer and Munro (1982; Accessory Publication).
[3] Data from Kailola and Wilson (1978: pp 23-37).
[4] Data from Cannon *et al.* (1987: Appendix II).
[5] Data from Russell (1983: Table 1).
[6] Data from Allen and Russell (1986).

Australia is not homogeneous. Broad variation between areas can be interpreted largely in terms of geographic and environmental factors. The North-west Shelf and Arafura Sea are similar, more or less continuous, open shelf environments. Their fish faunas are typical of offshore waters and both areas are dominated by carangids, lutjanids, carcharhinids, nemipterids, platycephalids, serranids, scorpaenids and bothids. The Gulf of Carpentaria and Gulf of Papua on the other hand contain extensive shallow areas that are subject to wide ranges of temperature and salinity, and their fish faunas comprise a mixture of euryhaline, semidiadromous and marine species (Kailola and Wilson 1978; Rainer and Munro 1982; Rainer 1984). Families that characterise these gulf areas include carangids, clupeids, scorpaenids, apogonids, leiognathids, ariids, sciaenids, and tetraodontids. Coastal Queensland differs from other shelf areas in that it is a sheltered, inner shelf environment, largely enclosed by the Great Barrier Reef. Dominant families characteristic of coastal Queensland include scorpaenids, carangids, bothids, tetraodontids, platycephalids and apogonids, as well as several groups (callionymids, monacanthids, triacanthoidids and triglids) that are not dominant elsewhere. The Great Barrier Reef and Rowley Shoals/Scott Reef represent coral reef environments that are markedly different to those of soft-bottom shelf waters. Dominant families that jointly characterise coral reef areas include gobiids, labrids, pomacentrids, blenniids, apogonids, serranids, chaetodontids, and acanthurids. With the exception of apogonids and serranids, these fishes are rare on soft-bottoms.

Species composition. The number of species recorded for the Arafura Sea (527) is less than for the North-west Shelf (666), but is greater than for the south-eastern Gulf of Carpentaria (341 species), Gulf of Papua (355 species) and Queensland (285 species). In terms of species composition, nearly half the species recorded from the North-west Shelf (48.8%) and the south-eastern Gulf of Carpentaria (47.2%) are shared with the Arafura Sea, while only about one third of species from coastal Queensland (33%) are shared with the Arafura Sea, suggesting greater faunal affinity between northern and north-western Australia than between northern and north-eastern Australia. Faunal similarity between the Arafura Sea and the Gulf of Papua (15.5%) is very low, perhaps due to a strong fluvial influence in the Gulf of Papua and the presence of many typically euryhaline species.

Not unexpectedly, there is little similarity in species composition of Arafura Sea fishes and fishes of Rowley Shoals/Scott Reef (4.8%) and the southern Great Barrier Reef

Table 2. Comparison of the family and species composition of the fish fauna of the Arafura Sea with fish faunas of the N.W. Shelf[1], S. Gulf of Carpentaria[2], Gulf of Papua[3], Coastal Queensland[4], S. Great Barrier Reef[5], and Rowley Shoals/Scott Reef[6].

	Arafura Sea	N.W. Shelf	S. Gulf of Carpentaria	Gulf of Papua	Coastal Queensland	S. Great Barrier Reef	Rowley Shoals/ Scott Reef
No. families[7]	141	134	88	84	97	108	77
No. shared families	-	110	81	72	70	77	53
Percent families shared[8]	-	82.1	92	85.7	72.2	71.3	68.8
No. species	527	666	341	355	285	859[9]	688
No. shared species	-	325	161	55	94	99	33
Percent species shared[8]	-	48.8	47.2	15.5	33	11.5	4.8

[1] Data from Sainsbury *et al.* (1985: pp 328-350, regions A + B).
[2] Data from Rainer and Munro (1982: Accessory Publication).
[3] Data from Kailola and Wilson (1978: pp 23-37).
[4] Data from Cannon *et al.* (1987: Appendix II).
[5] Data from Russell (1983).
[6] Data from Allen and Russell (1986).
[7] No. families of other authors adjusted in some cases to reflect recent nomenclatural changes.
[8] Percent families/species shared = n_c/n_x * 100, where n_c is the number of families/species in common with the Arafura Sea, and n_x is the number of species in the area being compared.
[9] Estimated total number of species for the whole Great Barrier Reef is 1300 (Russell, 1983).

(11.5%). The higher proportion of species in common with the southern Great Barrier Reef is due largely to inclusion of some trawl fishes among species recorded from this area. Jones and Derbyshire (1988) also found little similarity between fish species of the Great Barrier Reef and trawled fishes from coastal Queensland, and concluded that coral reef fish faunas are largely discrete from those of the adjacent benthic environment. This appears to be true also of Arafura Sea fishes: only 6.3% of Arafura Sea fishes occurred also at Rowley Shoals/Scott Reef. The occurrence of reef-associated species on soft-bottoms appears to be largely due to the presence of encrusting epifauna. On the North-west Shelf, some typical reef fishes (e.g. *Lethrinus, Lutjanus*) tend to be associated with sponge/gorgonian-dominated habitats (Sainsbury 1987), and similar associations of reef fishes with sponge bottoms have been reported in the tropical W. Atlantic (Collette and Rützler 1977).

Information which we present here deals only with fishes from offshore localities of the Arafura Sea and does not include data on depth distributions. However, variation in species composition between nearshore, shallow offshore, and deep offshore soft-bottom benthos areas, has been reported for both the Gulf of Carpentaria (Rainer and Munro 1982) and the Great Barrier Reef (Cannon *et al.* 1987), though differences between the assemblages were not clear-cut. Blaber *et al.* (1985) on the other hand found virtually no overlap in the inshore fish fauna of the Dampier region with deeper waters of the North-west Shelf. We would expect that more detailed study of patterns of distribution of Arafura Sea fishes will reveal similar cross-shelf differences in fish assemblages.

ZOOGEOGRAPHIC AFFINITIES

Indo-West Pacific. The fish fauna of tropical continental shelves shows a remarkable consistency, and many of the same families are represented over similar bottom types and in similar water masses throughout the tropics (Longhurst and Pauly 1987).

In terms of family composition, the fish fauna of the Arafura Sea shows strong similarities to that of other areas of the Indo-West Pacific such as the Andaman Sea and the Gulf of Thailand, prior to heavy exploitation (Pauly 1979). The dominant fish families of these areas and the Arafura Sea are typical of fish assemblages which occur on sandy offshore grounds in depths of 50-100m (Longhurst and Pauly 1987).

At the species level, there are also indications of similarities, with many species that occur in the Andaman Sea and Gulf of Thailand occurring also in the northern Australia. However, the taxonomic information available on demersal fish assemblages elsewhere is insufficient to make any detailed comparison with the Arafura Sea.

Australia. The fishes of the Arafura Sea have been included by Australian zoogeographers as part of the Dampierian faunal Province (Hedley 1926; Whitley 1932), an area which extends from Houtman's Abrolhos to Torres Strait. The Dampierian Province has been generally accepted by most workers (Bennett and Pope 1953; Knox 1963), although Endean (1957) concludes that it is doubtful whether separation of the Dampierian Province and Solanderian Province, which includes coastal Queensland (Banksian Province of Whitley 1932), is justified.

In a recent review of marine zoogeographic zones, Wilson and Allen (1987) found faunistic differences between the east and west coasts of northern Australia: on the eastern coast of Queensland there is a western Pacific element not present on the North-west Shelf, while conversely on the North-west Shelf there are a number of Indian Ocean and Indo-Malay species present which do not occur in Queensland. They also found significant endemicity (about 13% of species) in the fishes of northern Australia, with about 40% of the endemics restricted to the east coast and Great Barrier Reef, 30% from seas west of Cape York, and 30% widespread across northern Australia. However, they concluded that the faunal distinction between east and west appears to be mainly ecological (*i.e.* greater coral reef development in the north-east), although they conceded historical factors also are involved. Prior to the last Pleistocene flooding of the shelf area between Australia and Papua New Guinea, the North-west Shelf and the Queensland Shelf must have been relatively isolated from each other for long periods, this leading to faunistic differences (Wilson and Allen 1987).

Our comparison of family and species composition of Arafura Sea fishes with the

fish faunas of other areas of northern Australia generally agrees with that of Wilson and Allen (1987), and indicates greater faunistic affinity with the North-west Shelf than with coastal Queensland. However, many fish species are widely distributed across northern Australia and the distinction between the faunas of the North-west Shelf and Arafura Sea, and coastal Queensland is not clear-cut. Evidence from other studies (Rainer and Munro 1982; Sainsbury 1987; Longhurst and Pauly 1987) indicates that environmental factors such as the type of bottom deposits, occurrence of reefs, brackish and estuarine conditions, water depth, and differences in water masses are important determinants of species composition of demersal fish assemblages. We suggest that such environmental factors have had, and continue to have, a major influence in determining faunal differences between areas of northern Australia, and that these differences have largely overridden past vicariance events. For this reason, we draw short of recognising distinct zoogeographic regions for northern Australia.

IMPORTANCE TO FISHERIES.

Of the 527 species recorded (Appendix 1), 491 (93.2%) were taken by bottom trawl or dredge; 44 (8.3%) by gillnet; 19 (3.6%) by longline; 3 (0.6%) by handline; 4 (0.8%) were from deck strandings (all flying fishes, family Exocoetidae); and 1 (0.2%) by midwater trawl. While not all of the above categories are mutually exclusive, and some species were taken by more than one method, the overwhelming preponderance of species taken by trawling largely reflects the very high diversity of bottom-living fishes in the Arafura Sea.

Some 231 species were recorded from trawl samples taken from Taiwanese and Thai vessels operating in the Arafura Sea (Appendix 1, indicated by the symbol + after method of capture). Including species taken by also by gill net and handline, 108 species (20.5% of total species) are retained as catch (Appendix 1, shown in bold type) by commercial vessels. The remaining by-catch species that occur in commercial catches are discarded as trash. Based on their utilisation in fisheries elsewhere (Fischer and Bianci 1984), we have identified 163 discarded species (30.9% of total species) that are potentially useful for food (fresh, in fish cakes, or salted and dried), bait, or processing as fish meal and petfood (Appendix 1, indicated by an asterisk after method of capture). Whether or not utilisation of these by-catch species is likely to be economically viable, however, remains to be investigated.

Table 3. Dominant species taken by commercial trawlers in the Arafura Sea ranked in order of their contribution to the mean total catch biomass (%). Only species contributing $\geq$ 1% of total biomass are included. Discarded species are shown in bold type; other species are retained as catch. Data from Houston and Russell (in prep.).

Species	% of catch biomass
Lutjanus malabaricus Schneider	15.13
Nemipterus hexodon (Quoy and Gaimard)	6.60
Arius thalassinus (Rüppell)	4.73
Priacanthus tayenus Richardson	3.98
Nemipterus furcosus (Valenciennes)	3.88
Psenopsis anomala (Temminck and Schlegel)	3.87
Lethrinus lentjan (Lacepède)	3.76
Saurida micropectoralis Shindo and Yamada	3.49
Lutjanus erythropterus (Bloch)	2.77
Diagramma pictum (Thunberg)	2.74
Carcharhinus dussumieri (Müller and Henle)	2.63
Sphyraena putnamiae Jordan and Seale	1.65
Lutjanus vitta (Quoy and Gaimard)	1.63
Carangoides caeruleopinnatus (Rüppell)	1.57
Carangoides talamparoides Bleeker	1.49
***Terapon theraps* (Cuvier)**	**1.47**
Carangoides malabaricus (Bloch and Schneider)	1.30
Selar boops (Cuvier)	1.29
Priacanthus macracanthus Cuvier	1.28
Saurida sp. 2 (118016)	1.22
Rastrelliger kanagurta (Cuvier)	1.22
Nemipterus nematopus (Bleeker)	1.17
***Sargocentron rubrum* (Forsskål)**	**1.08**
Total	69.95

Quantitative analysis of trawl catches (Russell and Houston, in prep.) shows the great majority of fish species in the Arafura Sea occur in relatively small numbers, and that most species individually contribute less than 1% of the mean total catch biomass. Only 23 species (Table 3) were abundant enough in trawl samples to individually contribute 1% or more of the mean total catch biomass. This small group of species comprises only 4.4% of total species, but are dominant in catches and together comprise 70% of the mean total catch biomass of the demersal trawl fishery.

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APPENDIX 1.
Checklist of fish species recorded from offshore in the Arafura Sea.

Species are arranged in systematic order by family. Numbers in parentheses following the genus name for some unidentified species refer to the CSIRO species code used by Sainsbury *et al.* (1985). Questionable or unconfirmed records are indicated by a ? before the record; uncertain identifications are indicated by a ? following the species citation. Nomenclatural or taxonomic remarks are enclosed by square brackets following the family or species record. Records are based on specimens in the Northern Territory Museum, unless otherwise indicated. For abbreviations used for species records see Methods. Species retained in commercial catches are indicated in **bold** type; species taken by Taiwanese and Thai trawlers are indicated by a + symbol following method of capture; potentially important trawl species, presently discarded, are indicated by a * symbol following method of capture. Annotations indicate method of capture (BT, bottom trawl or dredge; GN, gill net; LL, longline; HL, handline; MT, midwater trawl; SD, stranded on deck; -, unknown).

FAMILY/Genus/species/author [Remarks]	Record	Method of capture
SQUALIDAE		
Squalus japonicus Ishikawa?		BT
ODONTASPIDIDAE		
Eugamphodus taurus **(Rafinesque)**		LL
PSEUDOCARCHARIIDAE		
?*Pseudocarcharius kamoharai* (Matsubara)	(Wei *et al.* 1972)	BT
[Recorded by Wei *et al.* (1972) as *Carcharius yangi* Teng, a junior synonym of *P. kamoharai* according to Compagno (1984)]		
ORECTOLOBIDAE		
Chilascyllium punctatum Müller and Henle		BT+
Eucrassarhinus dasypogon (Bleeker)		BT+
Nebrius concolor Rüppell	(CSIRO)	BT
Stegostama varium (Seba)	(CSIRO)	BT
SCYLIORHINIDAE		
Atelomycterus sp. (015005)		BT
Halaelurus sp. 1 (015004)		BT
LAMNIDAE		
?*Isurus oxyrinchus* Rafinesque	(Wei *et al.* 1972)	BT,GN
CARCHARHINIDAE		
Carcharhinus amblyrhynchoides **(Whitley)**	(CSIRO)	GN
C. amblyrhynchos (Bleeker)	(CSIRO)	BT*
C. ambainensis **(Müller and Henle)**	(CSIRO)	GN
C. brevipinna **(Müller and Henle)**	(CSIRO)	GN,LL
C. cautus (Whitley)	(CSIRO)	BT*
C. dussumieri **(Muller and Henle)**		BT+,GN
C. fitzroyensis **(Whitley)**	(CSIRO)	BT,GN
C. limbatus **(Müller and Henle)**	(CSIRO)	BT,GN,LL
C. macloti **(Müller and Henle)**	(FR)	BT+,GN, LL
C. melanopterus **(Quoy and Gaimard)**	(CSIRO)	BT,GN
C. obscurus **(Lesueur)**	(CSIRO)	BT,LL
C. plumbeus **(Nardo)**	(CSIRO)	BT,LL
C. sorrah **(Müller and Henle)**	(FR)	BT+,GN,LL
C. tilstoni **(Whitley)**	(Stevens and Wiley 1986)	BT,LL
Galeocerdo cuvieri **(Lesueur)**	(CSIRO)	BT,GN,LL
Negaprion acutidens (Rüppell)	(CSIRO)	BT*
Rhizoprionodon acutus **(Rüppell)**		BT+,GN,LL
R. taylori **(Ogilby)**		BT+,GN,LL
Triaenodon obesus (Rüppell)	(CSIRO)	BT*
HEMIGALEIDAE		
Hemigaleus microstoma **Bleeker**		BT+
Hemipristis elongatus **(Klunzinger)**	(CSIRO)	BT,GN,LL
SPHYRNIDAE		
Eusphyra blochii **(Cuvier)**	(CSIRO)	BT,GN,LL
Sphyrna lewini **(Griffith and Smith)**		BT+,GN,LL
S. mokarran **(Ruppell)**	(CSIRO)	BT,GN,LL
PRISTIDAE		
Pristis cuspidatus **Latham**	(CSIRO)	BT,GN
P. microdon Latham	(CSIRO)	BT*
P. zijsron Bleeker	(CSIRO)	BT*
RHYNCHOBATIDAE		
Rhina ancylostoma Bloch and Schneider	(CSIRO)	BT*
Rhyncobatus djiddensis **(Forsskål)**		BT+
RAJIDAE		
Raja sp.		BT
TORPEDINIDAE		
Narcine sp.		BT+
DASYATIDIDAE		
Amphostistius sp. 3 (035014)		BT
Dasyatis annotatus Last		BT+
D. kuhlii (Müller and Henle)		BT+
[Record of '*Trygon pastinaca* L.' by Günther (1880) probably refers to this species]		
D. leylandi Last		BT+
D. sephen (Forsskål)		BT
Himantura uarnak (Forsskål)		BT+
[*H. toshi* Whitley recorded from the Arafura Sea by Whitley (1940) is a junior synonym of *H. uarnak* according to Taylor (1964)]		
GYMNURIDAE		
Aetoplatea sp.		BT
Gymnura australis (Ramsay and Ogilby)		BT+
MYLIOBATIDIDAE		
Aetomyleus nichofii (Bloch and Schneider)		BT+
MOBULIDAE		
Mobula diabola Fowler		GN
CHIMAERIDAE		
Hydrolagus sp. (042004)		BT
ELOPIDAE		
Elops australis Regan	(Lyle and Timms 1984)	GN
MEGALOPIDAE		
Megalops cyprinoides (Broussonet)		BT+,GN*
ALBULIDAE		
Albula neoguinaica Valenciennes		BT+*
NEMICHTHYIDAE		
Nemichthys scolopaceus Richardson		BT
MURAENIDAE		
Gymnothorax sp. 1 (060004)	(CSIRO)	BT

MURAENESOCIDAE
Muraenesox bagio (Hamilton-Buchanan) BT+
M. cinereus (Forsskål) BT+

NETTASTOMATIDAE
Saurenchelys sp. (065001) (CSIRO) BT

CONGRIDAE
Lumiconger arafura Castle and Paxton (CSIRO) BT
Rhynchoconger sp. (067001) (CSIRO) BT
Coloconger raniceps Alcock? BT

OPHICHTHIDAE
Muraenichthys sp. BT+
Neenchelys retropinna Smith and Böhlke (Smith and Böhlke 1983) BT

CLUPEIDAE
Amblygaster sirm (Walbaum) (FR) BT+*
Anodontostoma chacunda (Hamilton-Buchanan) (CSIRO) BT*
Dussumieria elopsoides Bleeker BT+*
?*Etrumeus teres* (De Kay)? (Wei *et al.* 1972) BT
[Recorded by Wei *et al.* (1972) as *Etrumeus micropus* (Temminck and Schlegel) a junior synonym of *E. teres* - Whitehead (1985)]
Herklotsichthys koningsbergeri (Weber and Beaufort) (CSIRO) BT*
H. lippa (Whitley) BT*
Ilisha lunula Kailola (CSIRO) BT*
?*I. melastoma* (Bloch and Schneider) (Wei *et al.* 1972) BT
[Recorded by Wei *et al.* (1972) as *Illisha indica* (Swainson), a junior synonym of *I. melastoma* - Whitehead (1985)]
Pellona ditchela Valenciennes (FR) BT+*
Sardinella albella (Valenciennes) BT+*
S. gibbosa (Bleeker) (CSIRO) BT*

ENGRAULIDIDAE
Papuengraulis micropinna Munro (CSIRO) BT*
Setipinna tenuifilis Valenciennes (CSIRO) BT*
Stolephorus indicus (van Hasselt) BT+*
Thryssa hamiltonii (Gray) (CSIRO) BT*
T. setirostris (Broussonet) (CSIRO) BT*

CHIROCENTRIDAE
***Chirocentrus dorab* (Forsskål)** BT+,GN

GONOSTOMATIDAE
Cyclothone sp. (AMS) MT
Gonostoma elongatum Günther (Günther 1878) –

CHAULIODONTIDAE
Chauliodus sloanii Bloch and Schneider (Günther 1887) –

ALEPOCEPHALIDAE
Alepocephalus sp.? BT
Bajacalifornia sp. BT
Talismania filamentosa Okamura and Kawanishi? BT

SYNODONTIDAE
Synodus sageneus Waite (CSIRO) BT
[Record of *Saurus intermedius* Agassiz by Günther (1880) probably also refers to this species according to Whitley (1943)]
S. tectus Cressey BT+
[Record of *Synodus similis* McCulloch from the Arafura Sea by Munro (1957a) probably is based on a misidentification of *S. tectus*.]
Trachinocephalus myops (Bloch and Schneider) (CSIRO) BT

HARPADONTIDAE
[Assignment of *Saurida* to this family follows Johnson (1982)]
Harpadon translucens Saville-Kent (CSIRO) BT*
Saurida longimanus Norman BT+*
***S. micropectoralis* Shindo and Yamada** BT+
?*S. tumbil* (Bloch) (Wei *et al.* 1972) BT
S. undosquamis (Richardson) BT*
[Also recorded as *S. grandisquamis* Gunther by Gunther (1880)]

S. sp. 1 (118006) BT+*
***S.* sp. 2 (118016)** BT+

CHLOROPHTHALMIDAE
Chlorophthalmus sp. (120005) (CSIRO) BT

PARALEPIDIDAE
Stemnosudis rothschildi Richards BT

MORIDAE
Physiculus nigrescens Smith and Radcliffe (Paulin 1989) BT
P. roseus Alcock? BT

GONORHYNCHIDAE
Gonorhynchus sp. (141002) (CSIRO) BT

CHANIDAE
***Chanos chanos* (Forsskål)** (FR) BT+

ARIIDAE
Arius bilineatus Valenciennes BT+*
A. leiotetocephalus Bleeker BT+*
?*A. maculatus* (Thunberg) (Wei *et al.* 1972) BT
***A. thalassinus* (Rüppell)** BT+
A. sp. (188002) (CSIRO) BT*

PLOTOSIDAE
Euristhmus lepturus (Günther) BT+*
E. nudiceps (Günther) BT+*

BATRACHOIDIDAE
Batrachomoeus trispinosus (Günther) (CSIRO) BT*

LOPHIIDAE
Lophiodes naresi (Günther)? BT
Lophiomus setigerus (Vahl) (CSIRO) BT

ANTENNARIIDAE
Antennarius hispidus (Bloch and Schneider) BT

TETRABRACHIIDAE
Tetrabrachium ocellatum Günther BT+

CHAUNACIDAE
Chaunax pictus Lowe? BT

OGCOCEPHALIDAE
Dibranchus sp.? BT
Halieutaea indica Annandale and Jenkins BT+
H. stellata (Vahl) (CSIRO) BT

BREGMACEROTIDAE
Bregmaceros japonicus Tanaka? BT
B. macclellandi Thompson (CSIRO) BT

OPHIDIIDAE
Hoplobrotula armata (Temminck and Schlegel) (CSIRO) BT
Sirembo imberbis (Temminck and Schlegel) BT+

CARAPIDAE
Onuxodon margaritiferae (Rendahl) BT+

MACROURIDAE
Coelorinchus sp. BT
Hymenocephalus sp. BT

EXOCOETIDAE
Cheilopogon cyanopterus (Valenciennes) SD
Cypselurus poecilopterus (Valenciennes) (Munro 1957b) –
Hirundichthys oxycephalus (Bleeker) SD
Parexocoetus brachypterus (Richardson) (Paradice and Whitley 1927) SD
P. mento (Valenciennes) SD

MELAMPHAIDAE
Scopelogadus mizolepis (Günther) (Günther 1878) –
[Described as *Scopelus mizolepis* Günther (1878) and recorded as *Melamphaeus mizolepis* by Günther (1887)]

DIRETMIDAE
Diretmoides parini Post and Quero BT

TRACHICHTHYIDAE		
Haplastethus melanopus (Weber)		BT
H. melanapterus Fowler		BT
MONOCENTRIDIDAE		
Manacentris japonicus (Houttuyn)	(CSIRO)	BT
HOLOCENTRIDAE		
?Myripristis murdjan (Forsskål)	(Wei *et al.* 1972)	BT
Sargacentron rubrum (Forsskål)		BT+*
CAPROIDAE		
Antigonia rubescens (Günther)		BT
A. rhomboidea McCulloch	(CSIRO)	BT
VELIFERIDAE		
Velifer hypselopterus Bleeker		BT+
FISTULARIIDAE		
Fistularia petimba Lacepède		BT+*
CENTRISCIDAE		
?Aealiscus strigatus (Gunther)	(Wei *et al* 1972)	BT
Centriscus scutatus Linnaeus	(CSIRO)	BT
SYNGNATHIDAE		
Hippocampus histrix Kaup		BT
Salegnathus lettiensis Bleeker	(CSIRO)	BT
Trachyrhamphus longirostris Kaup	(AMS)	BT
SCORPAENIDAE		
Apistaps caloundra (De Vis)	(CSIRO)	BT
Apistus carinatus (Bloch and Schneider)	(CSIRO)	BT
Brachypterais serrulata (Richardson)		BT+
Cottapistus cottoides (Linnaeus)		BT+
Dendrachirus brachypterus (Cuvier)		BT
Erosa erosa (Langsdorf)		BT+
Inimicus sinensis (Valenciennes)		BT+
Minaus pictus Günther	(Günther 1880)	BT
Neamerinthe sp.		BT+
Pterois russelli Bennett		BT+
Scarpaenodes smithi Eschmeyer and Rama Rao		BT+
Scorpaenapsis cirrhosa (Thunberg)	(CSIRO)	BT
Sebastapistes amplisquamiceps (Fowler)	(AMS)	BT
Setarches longimanus (Alcock)	(CSIRO)	BT
TRIGLIDAE		
Gargariscus prionocephalus (Dumeril)		BT*
Lepidotrigla grandis Ogilby	(CSIRO)	BT*
?L. punctipectoralis Fowler	(Wei *et al.* 1972)	BT
L. spiloptera Günther	(CSIRO)	BT*
L. sp. 1 (288016)		BT+*
L. sp. 2 (288015)		BT+*
Pterygotrigla hemisticta (Temminck and Schlegel)	(CSIRO)	BT*
P. ryukyuensis Matsubara and Hiyama		BT*
Satyrichthys rieffeli (Kaup)	(CSIRO)	BT*
S. welchi (Herre)		BT*
APLOACTINIDAE		
Xenaploactis sp.		BT+
PLATYCEPHALIDAE		
Bembras japonicus Cuvier	(CSIRO)	BT*
Elates ransonneti (Steindachner)		BT+*
?Grammaplites scaber (Linnaeus)	(Wei *et al.* 1972)	BT
Inegocia harrisii (McCulloch)		BT*
I. japonica (Tilesius) [Previously recorded by CSIRO as *Suggrundus isacanthus* (Cuvier)]	(CSIRO)	BT*
Platycephalus endrachtensis Quoy and Gaimard	(CSIRO)	BT*
P. indicus (Linnaeus)	(CSIRO)	BT*
P. malabaricus Cuvier?	(Günther 1880)	BT*
P. sculptus Günther	(Günther 1880)	BT*
Rogadius asper (Cuvier)		BT+*
R. pristiger (Cuvier)	(Knapp 1987)	BT*
Suggrundus bosschei (Bleeker)	(CSIRO)	BT*
S. macracanthus (Bleeker)		BT+*
S. rodricensis (Cuvier)		BT+*
S. sp. 1 (296018)		BT+*
PSYCHROLUTIDAE		
Psychralutes sp.		BT
DACTYLOPTERIDAE		
Dactyloptena macracanthus (Bleeker)		BT+
D. orientalis (Cuvier)	(CSIRO)	BT
D. papilio Ogilby		BT+
?D. peterseni (Nystrom)	(Wei *et al.* 1972)	BT
CENTROPOMIDAE		
Psammoperca waigiensis Cuvier	(CSIRO)	BT*
SERRANIDAE		
Centrogenys vaigiensis (Quoy and Gaimard)	(CSIRO)	BT
Cephalopholis boenack (Bloch)		BT+*
?C. sexmaculatus (Ruppell) [Recorded by Wei *et al* (1972) as *Cephalopholis coatesi* Whitley, a junior synonym of *C. sexmaculatus*]	(Wei *et al.* 1972)	BT
Epinephelus amblycephalus (Bleeker)		BT*
***E. areolatus* (Forsskål)**		**BT+**
?E. diacanthus (Valenciennes)	(Günther 1880)	BT*
***E. epistictus* (Temminck and Schlegel)**	**(FR)**	**BT+**
E. fasciatus (Forsskål)	(CSIRO)	BT*
***E. heniochus* Fowler**		**BT+**
E. morrhua (Valenciennes)		HL
E. quoyanus (Valenciennes)		BT*
***E. sexfasciatus* (Valenciennes)**		**BT+**
***E. suillus* (Valenciennes)**	**(FR)**	**BT+**
Plectranthias japonicus (Steindachner)	(CSIRO)	BT
***Plectropomus maculatus* (Bloch)**		**BT+**
PSEUDOCHROMIDAE		
Pseudochromis quinquedentatus (McCulloch)		BT+
GLAUCOSOMATIDAE		
Glaucosoma magnificum (Ogilby)	(CSIRO)	BT*
TERAPONTIDAE		
Pelates quadrilineatus (Bloch)	(CSIRO)	BT*
Terapon jarbua (Forsskål)		BT+*
T. theraps (Cuvier)		BT+*
PRIACANTHIDAE		
?Priacanthus cruentatus (Lacepède)	(Wei *et al* 1972)	BT
P. hamrur (Forsskål)	(CSIRO)	BT*
***P. macracanthus* Cuvier**		**BT+**
***P. tayenus* Richardson**		**BT+**
Pristigenys niphonia (Cuvier)	(CSIRO)	BT*
APOGONIDAE		
Apogon brevicaudatus Weber	(CSIRO)	BT
A. ellioti Day [*A. arafurae* Günther recorded by Günther (1880) is a synonym of *A. ellioti* - Weber and Beaufort (1929)]		BT+
A. fasciatus (Shaw in White) [This species previously was recorded as *A. quadrifasciatus* Cuvier, a junior synonym (Randall and Lachner 1986). *A. monogramma* Günther also is a junior synonym of *A. fasciatus* - Weber and Beaufort (1929)]		BT+
A. hartzfeldi Bleeker	(CSIRO)	BT
A. melanopus Weber	(CSIRO)	BT
A. nigripinnis Cuvier	(CSIRO)	BT
A. poecilopterus Cuvier		BT+
A. septemstriatus Günther		BT+
Rhabdamia gracilis (Bleeker)		BT+
ACROPOMATIDAE [Assignment of genera to this family follows Johnson (1984)].		
Acropoma japonicum Gunther	(CSIRO)	BT
Malakichthys elegans Matsubara and Yamaguchi		BT
M. sp. (311031)	(CSIRO)	BT
Synagrops philippinensis (Gunther)		BT+
SILLAGINIDAE		
Sillago maculata Quoy and Gaimard	(CSIRO)	BT*
S. lutea McKay [Previously recorded by CSIRO as *Sillago* sp. 1]	(CSIRO)	BT*
BRANCHIOSTEGIDAE		
?Branchiostegus japonicus (Houttyn)	(Wei *et al.* 1972)	BT
***B. sawakinensis* Amirthalingam**		**BT+**

LACTARIIDAE		
Lactarius lactarius (Bloch and Schneider)	(CSIRO)	BT*
RACHYCENTRIDAE		
Rachycentron canadus **(Linnaeus)**		BT+,GN
ECHENEIDIDAE		
Echeneis naucrates Linnaeus		BT+*
Remora brachyptera (Lowe)		LL
R. remora (Linnaeus)	(Lyle and Timms 1984)	GN
CARANGIDAE		
Absalom radiatus (Macleay)	(CSIRO)	BT*
Alectis ciliaris (Bloch)		BT+*
A. indicus (Ruppell)		BT+*
Alepes **sp. (337051)**		BT+
?*Atule djedaba* (Forrskål)	(Wei *et al.* 1972)	BT
A. mate **(Cuvier)**		BT+
Carangoides caeruleopinnotus **(Ruppell)**		BT+
C. chrysophrys **(Cuvier)**		BT+
C. equula (Temminck and Schlegel)	(CSIRO)	BT*
C. fulvoguttatus (Forsskål)	(CSIRO)	BT*
C. gymnostethus (Cuvier)		BT+*
C. hedlandensis **(Whitley)**	(FR)	BT+
C. humerosus **(McCulloch)**		BT+
C. molabaricus **(Bloch and Schneider)**		BT+
?*C. oblongus* Cuvier	(Wei *et al.* 1972)	BT
C. talamparoides **Bleeker**		BT+
Caranx bucculentus **Alleyne and Macleay**		BT+,GN
C. ignoblis **(Forsskål)**	(FR)	BT+
?*C. melampygus* Cuvier	(Wei *et al.* 1972)	BT
C. sexfasciatus **Quoy and Gaimard**	(FR)	BT+
C. ille Cuvier	(CSIRO)	BT*
"*Caranx*" *para* (Cuvier)	(CSIRO)	BT*
Decapterus macrosoma Bleeker		BT+*
?*D. muroadsi* (Temminck and Schlegel)	(Wei *et al.* 1972)	BT
D. russelli (Ruppell) [also recorded as *D. lajang* Bleeker, a junior synonym, by Wei *et al.* (1972)]		BT+*
?*Gnathanodon speciosus* (Forsskål)	(Wei *et al.* 1972)	GN
Megalaspis cordyla (Linnaeus)	(FR)	BT+*
Scomberoides commersonianus **Lacepède**	**(Walter 1981)**	**GN**
S. lysan (Forsskål)	(CSIRO)	BT*
S. tala (Cuvier)	(CSIRO)	BT*
S. tol (Cuvier)		BT+*
Selor boops **(Cuvier)**		BT+
S. crumenaphtholmus **(Bloch)**		BT+
Selaroides leptolepis **(Cuvier)**	(FR)	BT+
Seriolino nigrofosciota **(Ruppell)**		BT+
Ulua aurochs **(Ogilby)**		BT+
?*Uraspis helvola* (Forster in Bloch and Schneider)	(Wei *et al.* 1972)	BT
U. uraspis **(Gunther)**		BT,BT+
CORYPHAENIDAE		
Coryphaena hippurus Linnaeus		HL
FORMIONIDAE		
Porastromoteus niger **(Bloch)**		BT+,GN
MENEIDAE		
Mene maculata (Bloch and Schneider)		BT+*
LEIOGNATHIDAE		
Gazza minuta (Bloch)		BT+*
Leiognathus aureus Abe and Haneda	(CSIRO)	BT*
L. bindus (Valenciennes)		BT+*
L. blochii (Valenciennes)	(CSIRO)	BT*
L. decorus (De Vis)	(CSIRO)	BT*
L. elongatus (Günther)	(CSIRO)	BT*
L. equulus (Forsskål)		BT+*
L. fasciatus (Lacepède)		BT+*
L. leuciscus (Günther)	(CSIRO)	BT*
L. moretoniensis (Ogilby)		BT+*
L. smithursti (Ramsay and Ogilby)	(CSIRO)	BT*
L. splendens (Cuvier)	(CSIRO)	BT*
L. stercorarius Evermann and Seale?		BT+*
L. sp. (341003)	(CSIRO)	BT*
Secutor insidiator (Bloch)		BT+*
S. ruconius (Hamilton-Buchanan)	(CSIRO)	BT*

EMMELICHTHYIDAE		
?*Erythrocles schlegelii* Richardson	(Wei *et al.* 1972)	BT
CAESIONIDAE		
Coesia cuning **(Bloch)**		BT+
?*Pteracaesio chrysozona* (Cuvier)	(Wei *et al.* 1972)	BT
P. digramma (Bleeker)	(FR)	BT+*
LUTJANIDAE		
?*Aprion virescens* Valenciennes	(Wei *et al.* 1972)	BT
Lutjanus argentimaculatus **(Forsskål)**	(FR)	BT+
L. carponotatus (Richardson)	(CSIRO)	BT*
L. erythropterus **(Bloch)**		BT+
?*L. fulviflamma* (Forsskål)	(Wei *et al.* 1972)	BT
?*L. gibbus* (Forsskål)	(Wei *et al.* 1972)	BT
L. johni **(Bloch)**	(FR)	BT+
?*L. kasmira* (Forsskål)	(Wei *et al.* 1972)	BT
L. lemniscotus **(Valenciennes)**		BT+
?*L. lunulatus* (Park)	(Wei *et al.* 1972)	BT
L. lutjanus Bloch		BT+*
L. molobaricus **Schneider**		BT+
?*L. monostigma* (Cuvier)	(Wei *et al.* 1972)	BT
L. quinquelineatus **Bloch**		BT+
L. rivulatus (Cuvier)		BT+*
L. russelli **(Bleeker)**		BT+
L. sebae **(Cuvier)**		BT+
L. vitto **(Quoy and Gaimard)**		BT+
?*Paracaesio xanthurus* (Bleeker)	(Wei *et al.* 1972)	BT
?*Pristipomoides argyrogrammicus* (Valenciennes)	(Wei *et al.* 1972)	BT
P. multidens **(Day)**		BT+,LL
NEMIPTERIDAE		
Nemipterus bathybius Snyder	(CSIRO)	BT*
N. celebicus **(Bleeker)**		BT+
N. furcosus **(Valenciennes)**	(FR)	BT+
N. hexodon **(Quoy and Gaimard)**		BT+
N. isacanthus **(Bleeker)**		BT+
N. marginatus (Valenciennes)		BT+*
N. nemotopus **(Bleeker)**		BT+
N. peronii **(Valenciennes)**		BT+
N. virgatus **(Houttuyn)**		BT+
N. zysron (Bleeker)	(Russell 1986a)	BT*
?*Parascolopsis eriomma* (Jordan and Richardson)	(Wei *et al.* 1972)	BT
P. rufomaculatus Russell	(Russell 1986b)	BT
Pentapodus porosus (Valenciennes)	(CSIRO)	BT
Scolopsis monogramma (Kuhl and Van Hasselt in Valenciennes) [This species has been misidentified by some authors as *S. temporalis*]	(FR)	BT+*
S. toeniopterus **(Kuhl and Van Hasselt in Valenciennes)**		BT+
S. vosmeri (Bloch)		BT
GERREIDAE		
Gerres filamentosus Cuvier		BT+*
G. kapas Bleeker?		BT+*
G. subfasciatus Cuvier	(CSIRO)	BT*
Pentaprion longimanus (Cantor)		BT+*
HAEMULIDAE		
Diogromma pictum **(Thunberg)**		BT+
Haplogenys kishinouyei Smith and Pope	(CSIRO)	BT*
?*Pomadasys argenteus* (Forsskål)	(Wei *et al.* 1972)	BT
?*P. hasta* (Bloch)	(Wei *et al.* 1972)	BT
P. kaakan **(Cuvier)**	(FR)	BT+
P. maculatum (Bloch)	(CSIRO)	BT*
LETHRINIDAE		
?*Gymnocranius griseus* (Temminck and Schlegel)	(Wei *et al.* 1972)	BT
G. robinsoni (Gilchrist and Thompson)		BT+*
Lethrinus froenotus **Valenciennes**		BT+
L. kallopterus Bleeker		HL
L. lentjan **(Lacepède)**		BT+
?*L. mahsenoides* Valenciennes	(Wei *et al.* 1972)	BT
?*L. miniatus* (Forster in Bloch and Schneider)	(Wei *et al.* 1972)	BT
L. nematacanthus Bleeker	(FR)	BT+*
?*L. ramak* (Forsskål) [Recorded by Wei *et al.* (1972) as *Lethrinus obsoletus* (Forsskål), a junior synonym of *L. ramak* - see Smith (1986)]	(Wei *et al.* 1972)	BT

SPARIDAE		
Argyraps spinifer (Forsskål)		BT+
SCIAENIDAE		
Argyrosomus amoyensis (Bleeker)		BT*
A. sp. (354012)		BT+
Atrobucca nibe (Jordan and Thompson)		BT*
Austranibea aedogenys Trewavas		BT*
Johnius coitor (Hamilton)	(CSIRO)	BT*
J. vogleri (Bleeker)		BT+*
Pratanibea diacanthus (Lacepède)		BT+
MULLIDAE		
?*Parupeneus chryserydros* (Lacepède) [This species was recorded as *Parupeneus luteus*, a synonym of *P. chryserydros* - see Kühlmorgen-Hille and Guézé (1974)]	(Wei *et al.* 1972)	BT
P. chrysopleuron (Schlegel)		BT+*
P. cinnabarinus (Cuvier)		BT+
?*P. janseni* (Bleeker)	(Wei *et al* 1972)	BT
?*P. trifasciatus* (Lacepède)	(Wei *et al* 1972)	BT
Upeneoides sp.	(Günther 1880)	BT*
Upeneus asymmetricus Lachner	(CSIRO)	BT*
U. bensasi (Temminck and Schlegel)		BT+*
U. luzanius (Jordan and Seale)	(CSIRO)	BT*
U. moluccensis (Bleeker)		BT+*
U. sulphureus (Cuvier)		BT+*
U. sundaicus (Bleeker)	(CSIRO)	BT*
U. tragula Richardson	(CSIRO)	BT*
U. sp. (355008)		BT+*
LEPTOBRAMIDAE		
Leptobrama muelleri Steindachner	(Lyle and Timms 1984)	GN
EPHIPPIDIDAE		
Drepane punctata (Linnaeus)	(CSIRO)	GN
?*Ephippus orbis* (Bloch)	(Wei *et al.* 1972)	BT
Platax batavianus Cuvier		BT+
P. teira (Forsskål)		BT+*
Zabidius navemaculeatus (McCulloch)		BT+*
CHAETODONTIDAE		
Chaetodan aureofasciatus Macleay	(CSIRO)	BT
C. modestus Schlegel	(CSIRO)	BT
?*C. unimaculatus* Bloch	(Wei *et al.* 1972)	BT
Chelmon marginalis Richardson	(CSIRO)	BT
C. muelleri (Klunzinger)	(CSIRO)	BT
Coradion altivelis McCulloch	(CSIRO)	BT
C. chrysozonus (Cuvier)		BT+
Heniochus acuminatus (Linnaeus)		BT+
Parachaetodon ocellatus (Cuvier)		BT+
POMACANTHIDAE		
?*Apolemichthys trimaculatus* (Cuvier)	(Wei *et al.* 1972)	BT
Chaetodontoplus duboulayi (Günther)		BT+
C. persanifer (McCulloch)		BT+
Pomacanthus sexstriatus (Cuvier)	(CSIRO)	BT
PENTACEROTIDAE		
Hystiapterus typus Temminck and Schlegel	(CSIRO)	BT*
POMACENTRIDAE		
Pristatis jerdoni (Day)		BT+
CEPOLIDAE		
Owstonia sp.		BT
SPHYRAENIDAE		
Sphyraena farsteri Cuvier		BT+
S. abtusata Cuvier		BT+
S. putnamiae Jordan and Seale		BT+
?*S. qenie* Klunzinger	(Wei *et al* 1972)	BT
POLYNEMIDAE		
Eleutheranema tetradactylum (Shaw)	**(Lyle and Timms 1984)**	**GN**
Palydactylus multiradiatus (Günther)		**BT+**
P nigripinnis Munro	(CSIRO)	BT*
Polynemus sheridani Macleay	**(Lyle and Timms 1984)**	**GN**
LABRIDAE		
Choerodon cauteroma Gomon and Allen		BT+*
C. cephalotes (Castlenau)	(CSIRO)	BT*

C. monostigma (Ogilby)		BT+*
C. schoenleinii (Valenciennes)	(CSIRO)	BT*
C. sugillatum Gomon		BT*
Xiphocheilus typus (Bleeker) [Also recorded as *X. quadrimaculatus* Günther by Günther (1880) a junior synonym - Gomon pers. comm.]		BT+
OPISTOGNATHIDAE		
Opisthognathus latitabundus (Whitley)		BT+*
O. sp.		BT*
PINGUIPEDIDAE		
Parapercis nebulosa (Quoy and Gaimard)	(CSIRO)	BT*
PHOLIDICHTHYIDAE		
Pholidichthys sp.		BT+
URANOSCOPIDAE		
Ichthyoscopus fasciatus Haysom	(CSIRO)	BT
Uranoscopus cognatus Cantor		BT+
U. fuscomaculatus Kner	(Günther 1880)	BT
U. kaianus Günther	(Günther 1880)	BT
?*U. oligolepis* (Bleeker)	(Wei *et al* 1972)	BT
U. sp. 2 (400016)	(CSIRO)	BT
U. sp. 1 (400009)		BT
CHAMPSODONTIDAE		
Champsodon arafurensis Regan?		BT+
BLENNIIDAE		
Xiphasia setifer Swainson		BT
CONGROGADIDAE		
Congrogadoides spinifer Borodin		BT+
CALLIONYMIDAE		
Callionymus belcheri Richardson [Previously misidentified as *C. longicaudatus* Schlegel by Günther (1880) fide Fricke (1983)]		BT
C. japonicus japonicus Houttyn		BT+
C. limiceps Ogilby	(CSIRO)	BT
C. keeleyi Fowler		BT+
C. octostigmatus Fricke		BT
C. sublaevis McCulloch	(CSIRO)	BT
Synchiropus delandi Fowler		BT
S. altivelis (Temminck and Schlegel)?		BT
GOBIIDAE		
Amoya sp. a		BT+
A. sp. b		BT+
A. sp. c		BT+
Bathygobius sp.		BT+
Lobulogobius morrigu Larson	(Larson 1983)	BT
Lubricogobius ornatus Formanoir		BT+
Priolepis sp. [Previously recorded as *Gobius* sp. by Günther (1889)]		BT+
P. sp. (*cf. nuchifasciatus*)		BT+
Sueviota larsonae Winterbottom and Hoese		BT+
AMBLYOPIDAE		
Amblyotrypauchen fraseri	(AMS)	BT
Brachyamblyopus sp.	(AMS)	BT
Ctenotrypauchen sp.		BT
ACANTHURIDAE		
Acanthurus grammoptilus Richardson		BT+*
SIGANIDAE		
Siganus fuscescens (Houttuyn)		BT+*
GEMPYLIDAE		
Neoepinnula orientalis (Gilchrist and von Bonde)	(CSIRO)	BT*
Rexea sp. (439002)	(CSIRO)	BT*
TRICHIURIDAE		
Tentoriceps cristatus (Klunzinger)	(CSIRO)	BT
Trichiurus lepturus Linnaeus		BT+
SCOMBRIDAE		
Auxis thazard (Lacepède)	**(Lyle and Timms 1984)**	**GN**

Cybiosarda elegans **(Whitley)**	**(Lyle and Timms 1984)**	GN
Euthynnus affinis **(Cantor)**	**(Lyle and Timms 1984)**	GN
?Rastrelliger chrysozonus (Rüppell)	(Wei *et al.* 1972)	BT
R. kanagurta **(Cuvier)**		BT+,GN
Scomberamorus cammersan **(Lacepède)**	**(FR)**	BT+,GN
?S. guttatus **(Bloch and Schneider)**	**(Lyle and Timms 1984)**	GN
S. munrai **Collette and Russo** [This species was recorded by Walter (1981) as *S. niphonius* (Cuvier), which according to Collette and Nauen (1983) is a misidentification of *S. munroi*.]	**(FR)**	BT+,GN
S. queenslandicus **Munro**		BT+,GN
S. semifasciatus **(Macleay)**	**(Lyle and Timms 1984)**	GN
Thunnus tonggal **(Bleeker)**		GN
XIPHIIDAE		
Xiphias gladius Linnaeus		GN
ISTIOPHORIDAE		
Istiopharus platypterus **(Shaw and Nodder)**	**(Read and Ward 1986)**	GN,LL
Makaira indica **(Cuvier)**	**(Nakamura 1974)**	LL
CENTROLOPHIDAE		
Psenapsis anomala **(Temminck and Schlegel)**		BT+
NOMEIDAE		
?Cubiceps squamiceps (Lloyd)	(Wei *et al.* 1972)	BT
ARIOMMATIDAE		
Ariomma indica **(Day)**		BT+
PSETTODIDAE		
Psettodes erumei **(Bloch and Schneider)**		BT+
CITHARIDAE		
Brachypleura novaezealandiae Günther		BT+*
BOTHIDAE		
Arnoglossus tapeinosoma (Bleeker)		BT+
A. waitei Norman		BT+
Asterhombus sp.		BT+
Engyprosopon grandisquama (Temminck and Schlegel) [This species was originally described from the Arafura Sea as *Rhomboidichthys spilurus* by Günther (1880), but is a junior synonym of *E. grandisquama* according to Norman (1934)]	(Norman 1934)	BT*
Grammatobothus polyophthalmus (Bleeker)		BT+
Laeops parviceps Gunther		BT+
Pseudorhombus arsius (Hamilton)	(CSIRO)	BT*
P. diplospilus Norman		BT+
P. dupliciocellatus Regan	(FR)	BT+
P. elevatus Ogilby		BT+*
?P. pentophthalmus (Günther)	(Wei *et al.* 1972)	BT
P. spinasus **McCulloch**	**(FR)**	BT+
P. sp. (460035)	(CSIRO)	BT

PLEURONECTIDAE		
Samariscus sp.		BT+
SOLEIDAE		
Dexillichthys muelleri (Steindachner)		BT+
Zebrias quagga (Kaup)		BT*
CYNOGLOSSIDAE		
Cynoglossus macrophthalmus Norman	(CSIRO)	BT*
C. kopsi Bleeker	(Günther 1880)	BT*
C. sp. (463002)	(CSIRO)	BT*
C. sp. (463010)	(CSIRO)	BT*
Symphurus sp.		BT+*
TRIACANTHIDAE		
Triacanthus biaculeatus (Bloch)	(CSIRO)	BT
Trixiphichthys weberi (Chaudhuri)		BT+
TRIACANTHODIDAE		
Halimochirurgus centriscoides Alcock		BT
Macrorhamphosodes platycheilus Fowler		BT
Tydemania navigatoris Weber		BT
BALISTIDAE		
Abalistes stellaris (Lacepède)		BT+
MONACANTHIDAE		
Alutera monoceros (Linnaeus)		BT+*
Monacanthus chinensis (Osbeck)	(CSIRO)	BT*
Chaetoderma penicilligera Cuvier	(Günther 1880)	BT
Paramonacanthus filicauda (Günther)		BT+
P. japonicus (Tilesius)	(CSIRO)	BT
Pseudomonacanthus peroni (Hollard)	(CSIRO)	BT
OSTRACIIDAE		
Ostracion cubicus Linnaeus	(FR)	BT+
Rhyncostracion nasus (Bloch)		BT+
R. rhinorhynchus (Bleeker)		BT+
Tetrosomus gibbosus (Linnaeus)	(CSIRO)	BT
TETRAODONTIDAE		
Amblyrhynchotes spinosissimus (Regan)	(CSIRO)	BT
Anchisomus multistriatus Richardson		BT+
Arathron nigropunctatus (Bloch and Schneider)	(Günther 1880)	BT
A. stellatus (Bloch and Schneider)		BT+
Chelonodon patoca (Hamilton-Buchanan)	(CSIRO)	BT
Lagocephalus inermis (Temminck and Schlegel)		BT+
L. lunaris (Bloch and Schneider)		BT+
L. sceleratus (Gmelin)		BT+
L. spadiceus (Richardson)		BT+
Torquigener pallimaculatus Hardy		BT+
TRIODONTIDAE		
Triodon macropterus Lesson	(CSIRO)	BT
DIODONTIDAE		
Cyclichthys hardenbergi (Beaufort)	(CSIRO)	BT
Cyclichthys orbicularis (Bloch)		BT+
?Diodon holocanthus Linnaeus [This species was recorded as *D. maculifer* Kaup, a probable junior synonym of *D. holocanthus* (Leis 1978)]	(Wei *et al.* 1972)	BT
Tragulichthys jaculiferus (Cuvier)		BT+

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A NEW SPECIES OF *WURIA* K. VIETS FROM NORTHERN AUSTRALIA (ACARINA: ARRENURIDAE)

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ABSTRACT

Wuria boutit sp. nov. is described from three specimens collected in Fogg Dam, Northern Territory, Australia. A key to the known species of the genus is presented.

KEYWORDS: Acarina, Arrenuridae, *Wuria*, new species, northern Australia.

INTRODUCTION

The water mite family Arrenuridae currently includes seven Recent genera (Cook 1974), of which the most diverse is *Arrenurus* Dugès. This genus is widespread throughout the world, and although only 15 species have been described from Australia, many further species await description (Harvey, unpublished data). The only other arrenurid genus thus far encountered in Australia is *Wuria* K. Viets, which is represented by the new species described here from Fogg Dam, Northern Territory.

Only two species of *Wuria* have been previously described: *W. falciseta* K. Viets from Cameroon and Ghana, and *W. sumatrensis* (K. Viets) from Sumatra. Each species of the genus (including the one described below) are represented in collections by merely a few specimens, and males of the Sumatran species are currently unknown.

Methods follow Harvey (1987). The length/width ratios for each acetabular plate are calculated by dividing the maximum length of each plate by its maximum width. The ratios for *W. falciseta* and *W. sumatrensis* are taken from published illustrations in Cook (1974) and K. Viets (1916, 1935). The specimens of the new species, which are mounted on slides in glycerol gel, are lodged in the Northern Territory Museum, Darwin (NTM) and the Museum of Victoria, Melbourne (NMV).

SYSTEMATICS

Genus *Wuria* K. Viets

Wuria K. Viets, 1916: 365; K.O. Viets 1987: 825 (type species *Wuria falciseta* K. Viets, 1916, by original designation).

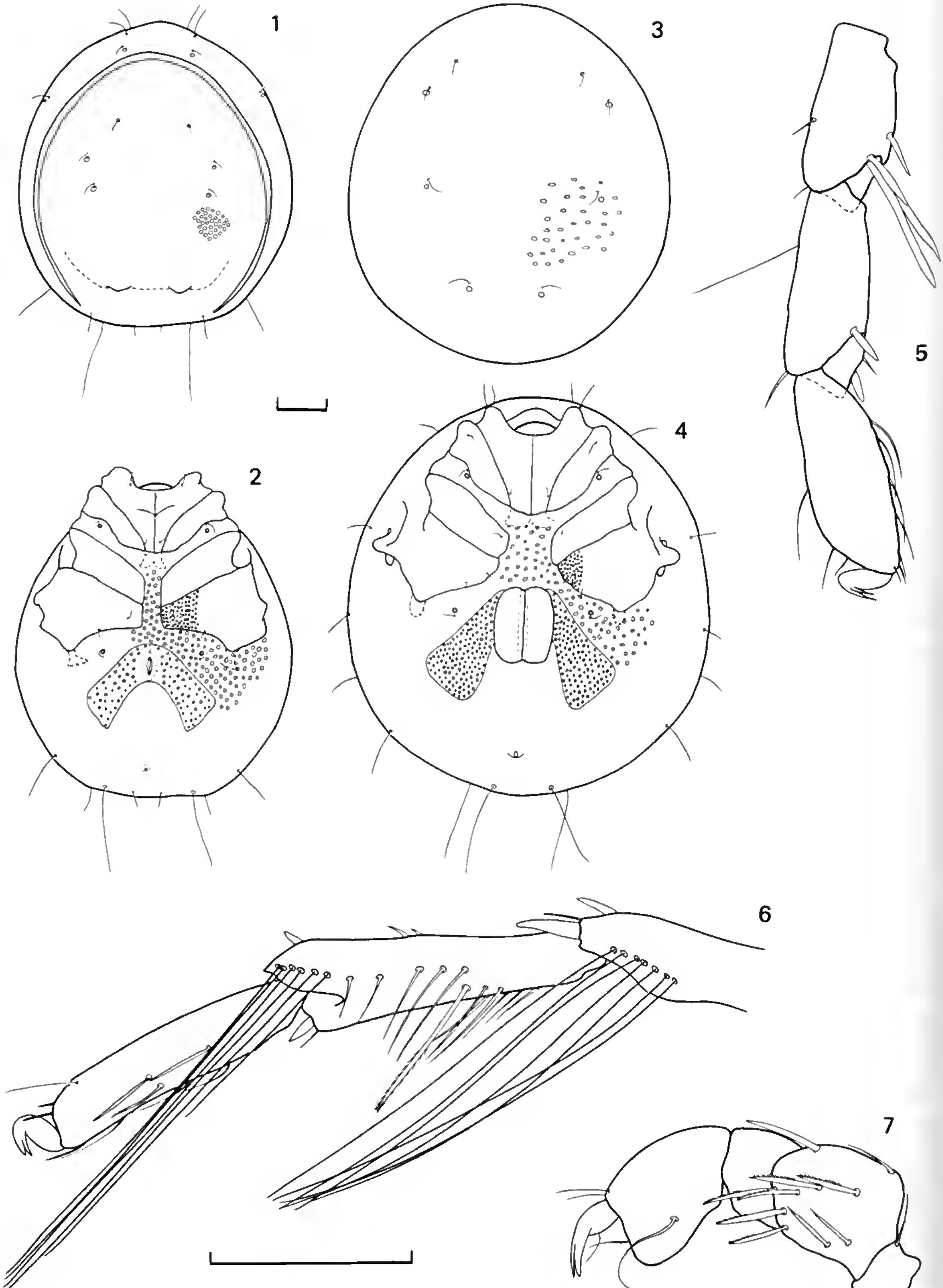
Wuriella K. Viets, 1935: 731 (type species *Wuriella sumatrensis* K. Viets, 1935). Synonymized by Cook (1974).

Diagnosis. Genital acetabula on indistinct plates, posteriorly directed. Capitular bay shallow. Antagonistic bristle of pedipalpal tibia long.

Remarks. The synonymy of *Wuriella* with *Wuria* by Cook (1974) was proposed provisionally pending the discovery of a male of the type species. Although males of *W. sumatrensis* remain undescribed, discovery of a new species of *Wuria* from northern Australia supports the proposed synonymy as females appear to be congeneric with those of both *W. falciseta* and *W. sumatrensis*.

Key to species of *Wuria*

1. Males (those of *W. sumatrensis* not known)..2
   Females..3
2(1). Each acetabular plate approximately 2.2 times as long as broad...*boutit* sp. nov.
   Each acetabular plate approximately 1.0 times as long as broad...*falciseta* K. Viets



Figs 1-7. *Wuria boutit*: Figs 1, 2, 5-7, holotype male; Figs 3, 4, paratype female: 1, dorsal aspect; 2, ventral aspect; 3, dorsal shield; 4, ventral aspect; 5, left leg I, genu, tibia and tarsus; 6, left leg IV, distal portion of genu, tibia and tarsus; 7, right pedipalp. Figs 1-4, to same scale; 5-7, to same scale. Scale lines 100 μm.

3(1). Distance separating dg2 greater than distance separating dg3 ....*sumatrensis* K.O. Viets
Distance separating dg2 approximately equal to distance separating dg3 4

4(3). Each acetabular plate approximately 1.7-1.9 times as long as broad ....*boutit* sp. nov.
Each acetabular plate approximately 1.1 times as long as broad.................... ....*falciseta* K. Viets

Wuria boutit sp. nov.
(Figs 1-7)

Type material. HOLOTYPE - male, Fogg Dam, Northern Territory, 13.vii.1987, M.S. Harvey and A.L. Yen, NTM A49. PARATYPES - 1 female, same data except 29.vi.1987, NTM A50; 1 female, same data, NMV K871.

Diagnosis. Acetabular plates narrow, each plate 2.15 (male), 1.71-1.89 (female) times as long as broad.

Description. *Adults*: Colour of male pale blue-green (specimen may be teneral), of female brilliant emerald green. Idiosoma (Figs 1-4): nearly round, 1.14 (male), 1.08-1.11 (female) x as long as broad; with conspicuous pores in male, with slightly less conspicuous pores in female; dorsal furrow of male incomplete, of female complete; dorsal shield with 3? (male), 3 (female) pairs of dorsoglandularia, and postocularia; distance separating dg2 approximately equal to that separating dg3; coxae I fused medially, faint suture line present; coxae III and IV separated from opposite members; suture line between coxae III and IV extending anterolaterally; coxa IV with well-developed condyles at insertions of leg IV. Acetabular plates indistinct, especially in female; extending posterolaterally from gonopore; each plate narrow, 2.15 (male), 1.71-1.89 (female) x as long as broad; total width of genital field 0.64 (male), 0.65-0.69 (female) x as long as broad. Capitular bay shallow; capitulum not fused with coxae. Pedipalp (Fig. 7): 5-segmented; uncate; slightly rotated; femur without dense patch of microsetae, but with 8-9 slightly serrate setae medially; antagonistic bristle of tibia very long. Legs (Figs 5-6): leg IV of male and female similar; telofemur, genu and tibia IV with small distal projections; tarsus IV slightly curved; with swimming setae arranged as follows: leg II: male, genu 3, tibia 4, female, genu 3, tibia 4; leg III: male, genu 5, tibia 6, female, genu 6, tibia 9; leg IV: male, telofemur 2, genu 7, tibia 6, female, telofemur 2, genu 7, tibia 12.

Dimensions (µm), male (female): dorsal shield 544/454 (719-735/623-656); ventral shield 621/544 (779-789/703-728); genital field 38/13 (154-160/125-131; pedipalp: trochanter 22 (25), femur 65 (70-73), genu 49 (52-55), tibia 75 (83-87), tarsus 35 (40-41); leg I: trochanter 78 (70), basifemur 62 (76-80), telofemur 73 (78-80), genu 88 (99), tibia 102 (118-119), tarsus 113 (127-132); leg IV: trochanter 123 (130-146), basifemur 109 (108-116), telofemur ? (118), genu 136 (159-166), tibia 177 (186-192), tarsus 153 (167-173).

Etymology. The specific epithet is an arbitrary combination of letters and is to be treated as an indeclinable noun.

Remarks. *Wuria boutit* differs from the two other described species of the genus by the narrow acetabular plates. In *W. boutit*, each acetabular plate is 2.15 (male), 1.71-1.89 (female) times as long as broad, in *W. falciseta* it is 0.99 (male), 1.08 (female) times as long as broad, while in *W. sumatrensis* it is 1.20 (female) times as long as broad.

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SIMOCEPHALUS SCHOEDLER (CLADOCERA:DAPHNIIDAE) IN TROPICAL AUSTRALIA

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ABSTRACT

Simocephalus latirostris Stingelin and *S. vetulus elisabethae* (King) are widespread in tropical Australia, whereas *S. acutirostratus* (King) is restricted to eastern Queensland and *S. serrulatus* (Koch) to the far north. Taxonomic comments are made on each species and a key for their identification is provided.

KEYWORDS: Cladocera, Daphniidae, *Simocephalus*, tropical Australia, distribution, new records.

INTRODUCTION

In a review of Australian Cladocera by Smirnov and Timms (1983), Dumont (1983) reported on the genus *Simocephalus* Schoedler, noting the presence of S. *vetulus elisabethae* (King), *S. vetulus gibbosus* (Sars), *S. latirostris* Stingelin, S. *exspinosus australiensis* (Dana), *S. acutirostratus* (King), and *S. victoriensis* Dumont. This assessment was based on collections mainly from southern Australia, with just a few from northeast Queensland. In a study of the biogeography of cladocerans in tropical Australia (Timms and Morton 1988; Timms 1988), four species of *Simocephalus* were recorded, including *S. serrulatus* (Koch), a new record for Australia. The purpose of this note is to make taxonomic comments on these species and to provide a key for their identification.

This study is based on collections from both the littoral and limnetic (if present) regions from 422 reservoirs, farm dams, lakes, billabongs and swamps throughout tropical Australia, except for the deserts of Western Australia and Northern Territory. Synonymies are restricted to only the original description and the latest description pertinent to Australia. Abbreviations used are: AM = Australian Museum, Bb = billabong, Ck = Creek, L = Lake, Lag = lagoon, MGU = Zoological Museum of Moscow University, NT = Northern Territory, NTM Cr. = Northern Territory Museum, Crustacea Department, Qld = Queensland, QM = Queensland Museum, R = River, Rd = Road, SA = South Australia, Sw = swamp, WA = Western Australia, WAM = Western Australian Museum, Wh = Waterhole, and Vic = Victoria. Unless otherwise indicated all material was collected by the author and is held in his collections.

Although a key is provided for all species of *Simocephalus* known from Australia, only those from tropical Australia are discussed here. Refer to Dumont (1983) for information on *S. expinosus australiensis* (Dana), which has been found only once in the tropics (by Sars, 1888 in central Qld), and on *S. victoriensis* Dumont, which so far has been recorded from central western Vic and southeastern SA.

Key to species of *Simocephalus* in Australia

1. Postabdominal claw with an outward basal pecten of enlarged spines.........2
   Spines on outward basal pecten of postabdominal claw not enlarged (at moderate magnification no pecten is visible)..4

2(1). Frons pointed.................................3
   Frons rounded..................................
   ....*exspinosus australiensis* (Dana)

3(2). Posterior of valves with a protuberance
   ....*acutirostratus* (King)
   Posterior of valves evenly rounded.....
   ....*victoriensis* Dumont

4(1). Frons angulate bearing short spines; ocellus small, rounded......*serrulatus* (Koch)
Frons rounded; ocellus large, elongated 5

5(4). Rostrum developed into a prominent 'nose'; ocellus rhomboidal. . . . .*latirostris* Stingelin
Rostrum short; ocellus sinuate and pointed at both ends................................ ....*vetulus* (O.F. Müller)

SYSTEMATICS

***Simocephalus vetulus* (O.F. Müller)**

Daphne vetula O. F. Müller, 1776: XXVII, 199, 275.

***Simocephalus vetulus elisabethae* (King)**
(Fig. 1E,F)

Daphnia elisabethae King, 1853a: 247-249, Pl. II.

Simocephalus vetulus elisabethae - Dumont 1983: 98-102, Figs 119, 120, Pl. I.

Material. (all females) QUEENSLAND: slides AM P35128, QM W11719, MGU 10254, Vardons Lag, 13°31'S, 142°27'E, 4.vii.1983; same data except pond 2km E of, 13°31'S, 142°28'E; same data except pond 4km E of, 13°31'S, 142°30'E; Pandanus Sw, 13°35'S, 142°34'E, 4.vii.1983; Mango Lag, 13°38'S, 142°34'E, 4.vii.1983; Cattle Sw, 14°54'S, 142°54'E, 26.vi.1983; same data except pond 1 km W of, 14°54'S, 142°54'E; same data except pond 1 km E of, 14°54'S, 142°55'E; same data except pond 2 km E of, 14°54'S, 142°55'E; Sw near Boggy L, 14°43'S, 143°46'E, 5.vii.1983; Sw near Saltwater Ck Crossing,14°47'S, 143°53'E, 6.vii.1983; Knifehole Lag, 14°36'S, 143°55'E, 6.vii.1983; pool near Hann R Crossing, 14°45'S, 144°02'E, 6.vii.1983; pool in Kennedy R Crossing, 14°46'S, 144°05'E, 6.vii.1983; Tea Tree Lag, 14°44'S, 144°07'E, 6.vii.1983; Sw 2 km NW of Lakefield Station, 14°55'S, 144°11'E, 6.vii.1983; Catfish Bb, 15°04'S, 144°17'E, 6.vii.1983; Little Kennedy L, 15°13'S, 144°37'E, 6.vii.1983; Horseshoe Lag, 15°16'S, 144°37'E, 7.vii.1983; L Emma, 15°17'S, 144°38'E,. 7.vii.1983; Jones Lag, 15°26'S, 145°10'E, 8.vii.1983; pool near Annan R Falls, 15°41'S, 145°12'E, 10.vii.1983; The Lake, Kings Plains Station, 15°41'S, 145°07'E, 10.vii.1983; New Years Day Lag, 15°40'S, 145°01'E, 10.vii.1983; Windermere Lag, 16°29'S, 143°20'E, 12.vii.1983; Mosquito Lag, 16°13'S, 142°55'E, 12.vii.1983; Swan Lag, 15°45'S, 142°55'E, 13.vii.1983; Red Lily Bb, 15°29'S, 142°48'E, 13.vii.1983; Sandy Bb, 15°29'S, 142°42'E, 13.vii.1983; unnamed lag near Barwon R, 16°52'S, 145°42'E, 23.vi.1983; unnamed lag at Rifle Ck, Mt. Molloy; 16°40'S, 145°19'E, 10.vii.1983; Emerald Ck Dam, 17°02'S, 145°30'E, 11.vii.1983; Dulbil Weir, 17°03'S, 145°29'E, 11.vii.1983; Nordellos Lag, 17°07'S, 145°25'E, 11.vii.1983; Eureka Ck, 17°11'S, 145°02'E, 11.vii.1983; a dam on Coolabbi Ck, 17°31'S, 145°29'E, 18.vi.1983; a farm dam 1 km S of Kaban, 17°32'S, 145°25'E, 18.vi.1983; same data except farm dam 2 km S of, 17°33'S, 145°25'E; a farm dam near Tumoulin, 17°34'S, 145°27'E, 20.vi.1983; Tablelands Tin Dam, 17°40'S, 145°06'E, 20.vi.1983; Spring Ck Dam, 17°43'S, 145°04'E, 20.vi.1983; Glencoe Lag, 17°22'S, 141°30'E, 14.vi.1983; Maggieville Lag, 17°27'S, 141°10'E, 14.vii.1983; Stake Lag, 17°32'S, 141°10'E, 14.vii.1983; Goose Lag, 17°39'S, 141°05'E, 17.vii.1983; The Lake Lag, 17°50'S, 141°08'E, 17.vi.1983; Wairuna Lag, 18°27'S, 145°19'E, 20.vi.1983; East Pelican L, 18°39'S, 145°08'E, 19.vi.1983; unnamed lag near Valley of Lagoons Homestead, 18°40'S, 145°06'E, 19.vi.1983; Horseshoe Lag, 20°05'S, 145°28'E, 12.vi.1983; Horse Lag, 20°04'S, 145°29'E, 12.vi.1983; Pink Lily Lag, 19°57'S, 145°37'E, 13.vi.1983; Red Lily Lag, 19°48'S, 145°55'E, 13.vi.1983; Horseshoe Lag, 19°33'S, 147°08'E, 17.vi.1983; Didjeridu Lag, 19°34'S, 147°15'E, 17.vi.1983; Payards Lag, 19°37'S, 147°19'E, 15.vi.1983; Gladys Lag, 19°53'S, 147°11'E, 15.vi.1983; same data except Sw near, 19°53'S, 147°11'E; Fowlers Lag, 19°44'S, 147°20'E, 14.vi.1983; Sw near Olsens Lag, 19°41'S, 147°29'E, 14.vi.1983; Berdaje Lag, 19°44'S, 147°29'E, 14.vi.1983; Flinders R at Richmond, 20°42'S, 143°08'E, 10.vii.1984; Nonda Ck at Nonda, 20°41'S, 142°28'E, 10.vii.1984; McIntyre Lag, 20°07'S, 141°20'E, 10.vii.1984; Corella Dam, 20°51'S, 140°02'E, 11.vii.1984; Spring Ck at Springvale Station, 23°34'S, 140°42'E, 12.vii.1984; Lion Lag, 23°22'S, 150°25'E,

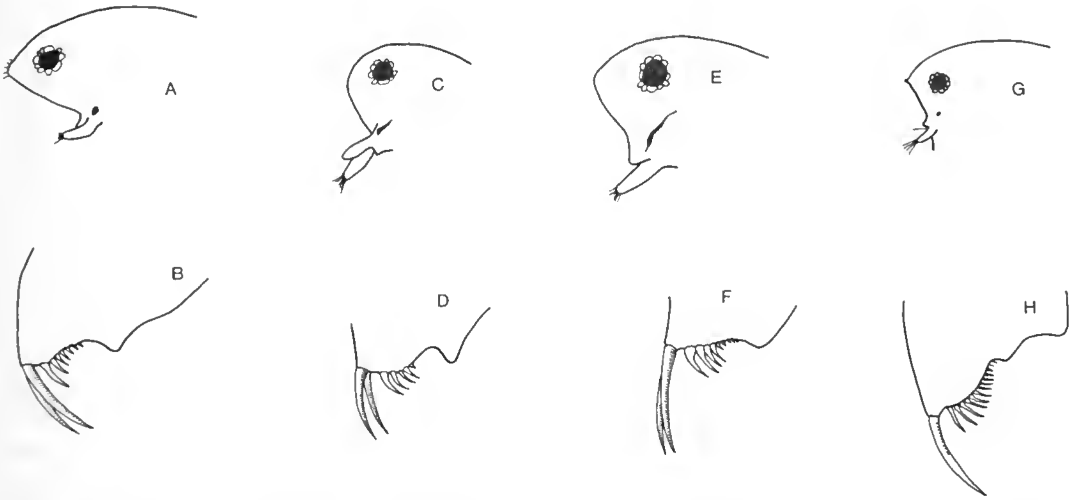

Fig. 1. *Simocephalus* spp. **A**, head and **B**, postabdomen of *S. serrulatus* female, length 2.6mm, from Joes Waterhole, Durack R. W.A., 5.x.1982; **C**, head and **D**, postabdomen of *S. latirostris* female, length 2.8mm, from a pool in Lydia Creek, Batavia Downs Station, Cape York Peninsula, Qld, 27.vi.1983; **E**, head and **F**, postabdomen of *S. vetulus elisabethae* female, length 2.2mm, from Sandy Billabong, Kowanyama, Cape York Peninsula, Qld, 13.vii.1983; **G**, head and **H**, postabdomen of *S. acutirostratus* female, length 3.8mm, from Horseshoe Lagoon, via Charters Towers, Qld, 12.vi.1983.

25.iv.1984; Crescent Lag, 23°25'S, 150°30'E, 25.iv.1984; unnamed Lag near Scrubby Ck, 23°25'S, 150°28'E, 25.iv.1984; Langley Ck, 23°27'S, 150°25'E, 25.iv.1984; same data except unnamed Lag near, 23°27'S, 150°25'E; Eight Mile Lag, 23°39'S, 150°40'E, 26.iv.1984.

NORTHERN TERRITORY: unnamed Bb by South Alligator R, 12°37'S, 132°25'E, 6.vii.1981; Fogg Dam, 12°34'S, 131°18'E, 6.vii.1981; Acacia Bb, 12°48'S, 131°12'E, 11.x.1982; same data except unnamed Lag near, 12°51'S, 131°12'E; unnamed Lag near Marrakai Crossing, 12°53'S, 131°12'E, 11.x.1982; unnamed Lag on Marrakai Rd, 12°55'S, 131°15'E, 11.x.1982; Darwin R Dam, 12°50'S, 130°59'E, 3.vii.1981; Manton Dam, 12°51'S, 131°08'E, 3.vii.1981; Little Red Lily Lag, 14°55'S, 133°26'E, 12.vii.1981; Adelaide R Crossing, 13°29'S, 131°04'E, 2.vii.1981; farm dam on Booroloola Rd, 16°44'S, 135°15'E, 13.vii.1981; Eight Mile Lag, 16°30'S, 136°14'E, 14.vii.1981; on slide AM P35129, NTM Cr. 2271, MGU 10255, Ormiston Gorge, 23°38'S, 132°44'E, 28.vi.1981; pool in the Valley of the Winds, 25°18'S, 130°45'E, 23.vi.1981.

Remarks. The status of Australian forms of the *vetulus* group has varied over the years. At present *S. elisabethae* King and *S. dulvertonensis* Smith are considered to be one subspecies (*elisabethae*), and *S. gibbosus* Sars another subspecies of *S. vetulus* (Dumont 1983). The only known difference between the two subspecies is the more strongly developed brood pouch in *S. gibbosus*, so that the upper posterior part of the valves is asymmetrically produced. However, juveniles of *S. vetulus elisabethae* also have a similar asymmetry (Houghton 1981), so adults are needed for positive identification. Almost all collections of *S. vetulus* from tropical Australia contained adults of *S. vetulus elisabethae*. The few collections in which only juveniles were present are therefore assumed to be of that subspecies also.

Distribution. In the Australian tropics *S. vetulus elisabethae* is absent from northwest WA, sparsely distributed in NT, and only common in eastern Qld (Fig. 3A). It seems to prefer well-vegetated billabongs and farm dams.

Simocephalus serrulatus (Koch)
(Fig. 1A,B, 2)

Daphnia serrulata Koch, 1841: 14.

Simocephalus serrulatus - Lilljeborg 1900: 179, Pl. XXVI, Figs 9-16.

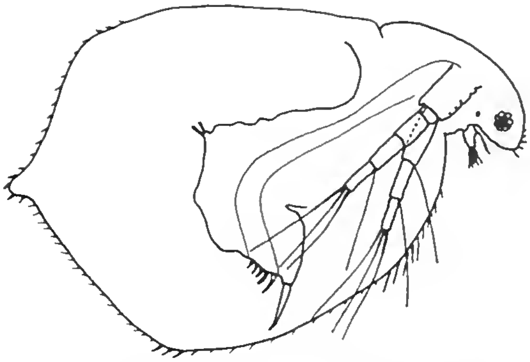

Fig. 2. *Simocephalus serrulatus* female, length 2.4mm, from Mudginberri Lagoon, Kakadu National Park, NT, 8.vi..1981.

Material. (all females) QUEENSLAND: a Lag near 6 Mile Yards, 14°55'S, 142°53'E, 26.vi.1983; on slides AM P35127, QM W11718, MGU 10251, pond 2km E of Cattle Sw, 14°54'S, 142°55'E, 26.vi.1983; Goolboo Lag, Silkwood, 17°43'S, 146°01'E, 24.vi.1983.

NORTHERN TERRITORY: on slides AM P35126, NTM Cr. 2270, MGU 10252, Mudginberri Lag, 12°35'S, 132°52'E, 8.vii.1981; Wh on Magela Ck, 12°35'S, 132°52'E, 8.vii.1981.

Remarks. This species is similar in many respects (e.g. structure and spination of postabdomen) to *S. vetulus*, but the angulate frons, which bears *ca.* 5 small, narrow spines on the angle and extending onto the upper side, and the small rounded or perhaps diamond-shaped ocellus, serve to distinguish it. The rostrum is also more developed in the present species, and the protuberance (= posterior spine of some authors) on the middle-posterior portion of the valves is more pronounced than in *S. vetulus elisabethae*. The protuberance of the latter is similar to that of S. *latirostris*.

Distribution. Sparse in the most northerly parts (Fig. 3C). All localities were shallow, well-vegetated and semi-permanent. These records are new for Australia.

Simocephalus latirostris Stingèlin
(Fig. 1C,D)

Simocephalus latirostris Stingelin, 1906: 187, Figs 5-7; Dumont 1983: 103-104, Figs 121, 122, Pl. 1,2.

Material. (all females) QUEENSLAND: pool near Moreton Telegraph Station, 12°27'S, 142°39'E, 27.vi.1983; on slides AM P35125, QM W11717, MGU 10250, pool in Lydia Ck, 12°40'S, 142°40'E, 27.vi.1983; pool in Plain Ck, 13°07'S, 142°26'E, 3.vii.1983; Chong Sw, 13°37'S, 142°35'E, 4.vii.1983; a Lag 4km W of Strathaven Station, 14°54'S, 142°46'E, 26.vi.1983, Sw near Boggy L, 14°43'S, 143°46'E, 5.vii.1983; pool in Long Waterhouse Ck, 14°47'S, 144°08'E, 6.vii.1983; Red Lily Lag, 14°51'S, 144°10'E, 6.vii.1983; pool near Morgan R, 15°06'S, 145°17'E, 8.vii.1983; pool near Melvor R, 15°09'S, 145°05'E, 8.vii.1983; Pooles Lag, 15°32'S, 145°11'E, 8.vii.1983; roadside ditch, 44km SW of Cooktown, 15°42'S, 145°04'E, 10.vii.1983; Dinner Camp Lag, 16°34'S, 143°31'E, 12.vii.1983; Windermere Lag, 16°29'S, 143°20'E, 12.vii.1983; Wh near Alberts Lag, 16°28'S, 143°15'E, 12.vii.1983; Widow Lag, 16°17'S, 143°00'E, 12.vii.1983; Dunbar Lag, 16°03'S, 142°22'E, 13.vii.1983; Wh near Rutland Plains Station, 15°40'S, 142°52'E, 13.vii.1983; Centenary L, Cairns, 16°55'S, 145°45'E, 21.vi.1983; Mulgrave R at Gordenvale, 17°06'S, 145°48'E, 21.vi.1983; pool in Stirling Ck, 17°13'S, 141°42'E, 14.vii.1983, a Wh on 8 Mile Ck, 17°25'S, 141°18'E, 14.vii.1983; unnamed lag, 4km S of Normanton, 17°40'S, 141°07'E, 17.vii.1983; Snakehole Wh, 17°45'S, 141°07'E, 17.vii.1983; same data except 4km N of, 17°43'S, 141°09'E; 12 Mile Lag, 17°51'S, 141°07'E, 17.vii.1983; pond near Bynoe R, 17°52'S, 140°48'E, 17.vii.1983; Wh at Inverleigh, 18°01'S, 140°34'E, 17.vii.1983; M Lag, 18°06'S, 140°17'E, 15.vii.1983; Judy Lag, 17°57'S, 139°35'E, 15.vii.1983; Old Station Wh, 17°56'S, 139°47'E, 15.vii.1983; Bullock Wh, 17°56'S, 139°45'E, 15.vii.1983; Yarrum Lag, 17°49'S, 139°34'E, 15.vii.1983; Harris Lag, 17°49'S, 139°33'E, 15.vii.1983; Woods Lag, 17°44'S, 139°30'E, 15.vii.1983; Gap Dam, 18°02'S, 140°02'E, 15.vii.1983; Fork yard Lag, 17°56'S, 140°10'E, 15.vii.1983; same data except a Wh near Saltern Lag, 18°41'S, 145°03'E, 19.vi.1983; same data except unnamed Lag S of; a dam 5km S of Camel Ck Station, 18°52'S, 145°30'E, 19.vi.1983; Farquesons Lag, 20°04'S, 145°26'E, 12.vi.1983; Dry Lag, 20°03'S, 14°30'E, 12.vi.1983;

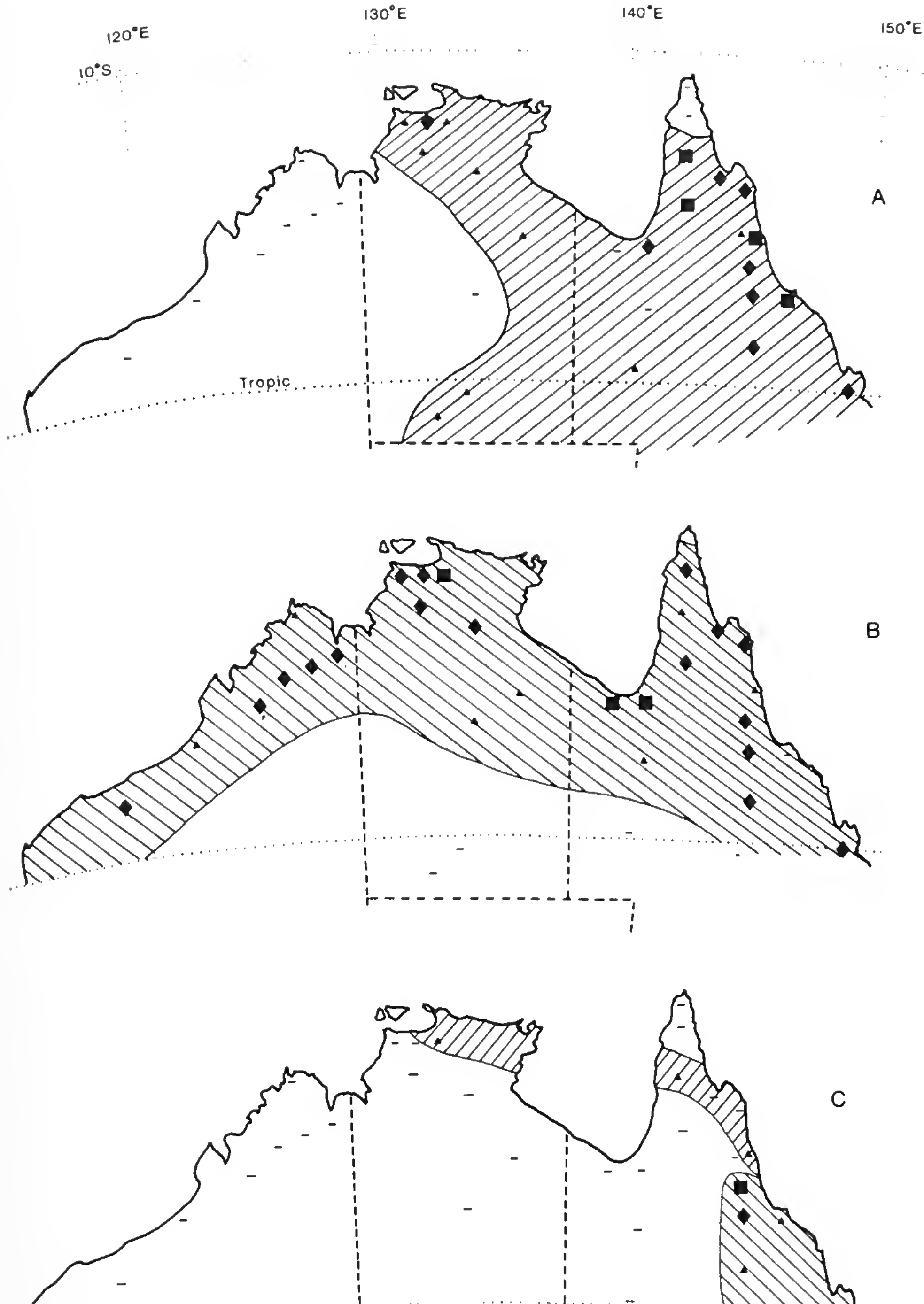

Fig. 3. Tropical Australia showing the distribution of **A**, *S. vetulus elisabethae*; **B**, *S. latirostris*; and **C**, *S. serrulatus* (acute oblique stripes) and *S. acutirostratus* (obtuse oblique stripes). Each symbol represents collections containing the nominated species in an area where 10-15 (mean 12.8) localities were sampled ▲ = 1-2 collections, ◆ = 3-5 collections, and ■ = 6 or more collections. Dashes indicate no specimens were caught in that area.

Toomba L, 20°01'S, 145°36'E, 12.vi.1983; Toomba Sw, 19°58'S, 145°36'E, 13.vi.1983; Reeves L, 19°53'S, 145°50'E, 12.vi.1983; pool near Patens L, 19°52'S, 145°59'E, 12.vi.1983; Natal Ck at Myrtna Station, 21°17'S, 146°14'E, 24.iv.1984; L Galilee, Oakvale Reach, 22°17'S, 145°56'E, 23.iv.1984; L Barcoorah, 22°31'S, 145°21'E, 22.iv.1984; a dam on Silver Hills Station, 20°37'S, 143°06'E, 10.vii.1984; a Lag near Edenbann Lag, 23°04'S, 150°07'E, 26.iv.1984; Canoona Lag, 23°07'S, 150°16'E, 26.iv.1984; Boomerang Lag, 23°14'S, 150°22'E, 26.iv.1984.

NORTHERN TERRITORY: Pool on South Alligator R, 12°37'S, 132°26'E, 6.vii.1981; Malabanbanju Lag, 12°26'S, 132°44'E, 6.vii.1981; Burulba Lag, 12°47'S, 132°45'E, 8.vii.1981; Mudjinberri Lag, 12°35'S, 132°52'E, 8.vii.1981; unnamed Bb, East Alligator R, 12°27'S, 132°58'E, 8.vii.1981; same data except 12°28'S, 132°59'E; Sandy Bb, 12°54'S, 132°46'E, 9.vii.1981; Fogg Dam, 12°34'S, 131°18'E, 6.vii.1981; Harrison Dam, 12°34'S, 131°20'E, 6.vii.1981; Wh near Beatrice Lag, 12°38'S, 131°19'E, 6.vii.1981; unnamed Lag near Acacia Bb, 12°49'S, 131°12'E, 11.x.1982; quarry near Howard Springs, 12°28'S, 131°04'E, 5.vii.1981; Quambi Lag, 12°23'S, 131°10'E, 5.vii.1981; McMinns Lag, 12°33'S, 131°05'E, 11.x.1982; Roper Valley Station Homestead Springs, 14°56'S, 134°00'E, 12.vii.1981; Duck Hole Bb, 14°44'S, 134°03'E, 12.vii.1981; Roper R near Roper Valley Homestead, 14°51'S, 134°01'E, 12.vii.1981; unnamed Lag near Little Red Lily Lag, 14°56'S, 133°25'E, 12.vii.1981; Roper R at Elsey Station, 14°58'S, 133°20'E, 12.vii.1981; Abraham Lag, 14°54'S, 133°04'E, 12.vii.1981; farm dam at Emerald Spring, 13°39'S, 131°38'E, 2.vii.1981; slides AM P35124, NTM Cr. 2269, MGU 10249, Survey Ck, 13°30'S, 130°56'E, 2.vii.1981; Yarra Bb, Daly R, 13°42'S, 130°39'E, 2.vii.1981; pool in Edith R, 14°11'S, 132°02'E, 9.vii.1981; Bessie Spring at MacArthur Station, 16°40'S, 135°51'E, 12.vii.1981; Leila Lag, 16°37'S, 135°42'E, 14.vii.1981; Wh at Larramah, 15°57'S, 133°27'E, 1.vii.1981.

WESTERN AUSTRALIA: Irrigation ditch, Kununurra, 15°45'S, 128°42'E, 7.x.1982; L Kununurra, 15°48'S, 128°42'E, 7.x.1982; pool in Ord R at Ivanhoe Crossing, 15°41'S, 128°41'E, 7.x.1982; Slides AM P35125, WAM 166-84, MGU 10250, pool in King R, 15°55'S, 128°07'E, 6.x.1982; Big Hole, Chamberlain R, 15°59'S, 127°56'E, 6.x.1982; Joes Wh, Durack R, 15°50'S, 127°42'E, 5.x.1982; pool 9 km W of Durack R Crossing, 15°58'S, 127°09'E, 5.x.1982; Dawn Ck, 15°59'S, 127°01'E, 5.x.1982; Airfield Sw, Mitchell Plateau, 14°46'S, 125°49'E, 19.ix.1982; Isdell R, 16°55'S, 125°34'E, 4.x.1982; Adcock R, 17°03'S, 125°42'E, 4.x.1982; Bell Ck, 17°10'S, 125°21'E, 4.x.1982; Windjana Gorge, 17°24'S, 124°57'E, 3.x.1982; Geike Gorge, 18°07'S, 125°42'E, 3.x.1982; unnamed Lag near Noonkanbah, 18°29'S, 125°04'E, 1.x.1982; 17 Mile Dam, Camballin, 18°03'S, 124°20'E, 1.x.1982; farm dam 24km NW Camballin, 17°55'S, 124°06'E, 1.x.1982; Sw near Yabbagooly Claypan, 17°22'S, 123°45'E, 1.x.1982; pool near Minnie R, 17°45'S, 123°35'E, 1.x.1982; Coongan R at Coongan Station, 20°42'S, 119°39'E, 28.ix.1982; Coongan R at Marble Bar, 21°11'S, 119°42'E, 28.ix.1982; Jones R, 20°59'S, 117°23'E, 26.ix.1982; White Spring Pool, George R, 21°08'S, 117°25'E, 26.ix.1982; Hooley Ck, 21°53'S, 118°00'E, 27.ix.1982.

Remarks. Apart from the obvious difference in the structure of the rostrum, *S. latirostris* differs from *S. vetulus elisabethae* in a number of other easily discernible features. Most useful are: (i) the shape of the ocellus: in *S. latirostris* it is basically rhomboidal with one end below the eye drawn out to a point and the end towards the rostrum triangular in shape, whereas in *S. vetulus elisabethae* it is sinuate, distinctly elongated and pointed at both ends; (ii) the postanal protuberance on the postabdomen is prominent and asymmetrical in *S. latirostris* and rounded and less pronounced in *S. vetulus elisabethae*; (iii) the protuberance on the middle posterior portion of the valves is more prominent in *S. latirostris*; and (iv) the head pores are situated on a tubercle in *S. latirostris* but lie in a depression in *S. vetulus elisabethae*.

Distribution. In Australia this species occurs mainly in the tropics, but it is uncommon in drier areas (eg. 90-Mile Desert in WA), in southern parts (as in NT and Qld), at higher altitudes (eg. Atherton Tableland, Qld), and in areas with distinctly acid waters (eg. tip of Cape York) (Fig. 3B). Outside the

tropics it is also known from central Qld (Dumont 1983) and from southwest WA (R. Shiel, pers. comm.).

Simocephalus acutirostratus (King)
(Fig. 1G, H)

Daphnia elisabethae var. *acuti-rostrata* King, 1853b: 254, Pl. VIc.

Simocephalus acutirostratus - Sars 1888: 67; 1896: 12-15, Pl. 2, Figs 1-3; Dumont 1983: 104-105, Fig. 124, Pl. 1,2.

Material. (all females) QUEENSLAND: Wairuna Sw, 18°27'S, 145°19'E, 20.vi.1983; Sw near Lucy Ck, 18°34'S, 145°18'E, 20.vi.1983; Sw at Lucy Station, 18°35'S, 145°16'E, 20.vi.1983; East Pelican Lag, 18°39'S, 145°08'E, 19.vi.1983; unnamed Lag just N of Valley of Lagoons Station Homestead, 18°40'S, 145°06'E, 19.vi.1983; same data except SW of, 18°41'S, 145°05'E; unnamed Lag near Burdekin R, 18°42'S, 145°04'E, 19.vi.1983; pool near Saltern Lag, 18°41'S, 145°03'E, 19.vi.1983; unnamed Lag near Myora Yards, 20°05'S, 145°28'E, 12.vi.1983; Horseshoe Lag, 20°05'S, 145°28'E, 12.vi.1983; Dry Lag, 20°03'S, 145°30'E, 12.vi.1983; Lolworth Sw, 19°59'S, 145°36'E, 13.vi.1983; Sw 2km N of Ayrville, 19°41'S, 147°20'E, 15.vi.1983; slides AM P35122, QM W11716, MGU 10253, L Galilee, 22°19'S, 145°51'E, 22.iv.1984.

Remarks. This large species (up to 4.2mm) is distinguished from other tropical species of *Simocephalus* by its pointed frons, small rounded to rhomboidal ocellus very close to the rostrum, broad postabdomen with two embayments and an anal corner forming a right angle, a rounded preanal protuberance, and an enlarged basal pecten on the postabdominal claw.

S. acutirostratus is separable from both of the other Australian species which have enlarged basal pectens by the pointed frons (absent in *S. exspinosus australiensis* and present as a finger-like projection in *S. victoriensis*). It further differs from *S. exspinosus australiensis* by having more enlarged spines in the pecten (12-18 cf. 8-12 in *S. exspinosus australiensis*) and from *S. victoriensis* by the shallow postabdominal embayments and smoothly rounded anal corner in this species.

Distribution. Localised along the coast and adjacent hinterland of Qld, from the vicinity of Townsville south to Bowen (Dumont 1983) (Fig. 3C), where it is typically found in broad, shallow (<50cm) ephemeral pools on floodplains.

DISCUSSION

Six species of *Simocephalus* are now known for Australia, with four occurring regularly in the tropics (Fig. 3). *S. serrulatus* occurs only in the far north of Qld and NT, and *S. latirostris* is widespread and indeed penetrates just south of the Tropic of Capricorn, west of Rockhampton (Dumont 1983), and is known from southwest WA (R. Shiel, pers. comm.). *S. vetulus elisabethae* is almost ubiquitous throughout Australia, although it has not been recorded from the northwest. Since it and *S. latirostris* are both abundant in well-vegetated billabongs in the tropics, but rarely co-occur, it is possible they have similar niches and may compete at times. Nevertheless, *S. latirostris* seems the better adapted of the two for tropical waters, as indicated by the greater variety of habitats it occupies, its wider distribution, and generally greater abundance in collections. *S. acutirostratus*, while found in much of southern and eastern Australia, is restricted in the tropics to eastern Qld around Townsville. Dumont (1983) considers that *S. acutirostratus* replaces the cosmopolitan *S. serrulatus* in Australia. Even though the latter is now known from northern Australia, the distributions of the two species do not overlap. Of the two southern species, *S. exspinosus australiensis* is widespread, particularly in southern and western areas, though there is an isolated old record by Sars (1888) from near Rockhampton. The remaining species, *S. victoriensis* occurs in central western Victoria and the adjacent part of South Australia.

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A NEW GENUS AND SPECIES OF COMMENSAL SCALEWORM (POLYCHAETA:POLYNOIDAE) FROM BROOME, WESTERN AUSTRALIA

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ABSTRACT

A new genus and species *Capitulatinoe cupisetis* gen.et sp.nov. from Broome, Western Australia is described. The new species is commensal, living in the ambulacral grooves of a starfish, *Astropecten granulatus* Müller and Troschel, 1842.

KEYWORDS: Polychaeta, Polynoidae, new genus, new species, commensal, Broome, Western Australia.

INTRODUCTION

Two visits to Broome, Western Australia, in 1984 and 1987 were undertaken for the purpose of collecting polychaetes for the Northern Territory Museum (NTM). Amongst the material collected, were a number of polynoid scaleworms found in the ambulacral grooves of the common starfish, *Astropecten granulatus*.

The scaleworms possess a unique set of characteristics distinguishing them from all existing genera and species of the family Polynoidae and therefore are described herein as a new genus and species.

SYSTEMATICS

Family Polynoidae Malmgren, 1867
Subfamily Arctonoinae Hanley, 1989
***Capitulatinoe* gen. nov.**

Type species *Capitulatinoe cupisetis* sp. nov.

Gender: feminine.

Diagnosis. Body elongate, subcylindrical in cross-section, fragile, with numerous segments (up to 181), without pigment. Elytra numerous pairs, on prominent elytrophores, on segments 2, 4, 5, 7, 9, alternate segments to 25, 26, 28, 29, 30, 32, 33, thereafter usually two elytragerous segments alternating with single cirrigerous segments to end of body, with some irregularity on posterior segments. Elytra large, soft, transparent. Prostomium hexagonal, truncate anteriorly, not bilobed, without cephalic peaks, with two pairs of eyes, paired palps, and three antennae. Ceratophore of median antenna inserted on distal end of prostomium; ceratophores of lateral antennae inserted slightly dorsal to ceratophore of median antenna. First or tentacular segment not visible dorsally; tentaculophores lateral and ventral to prostomium, achaetous, each with pair of dorsal and ventral tentacular cirri; without facial tubercle. Second or buccal segment with middorsal bulbous area, first pair of elytra on prominent elytrophores, subbiramous parapodia (notopodium much smaller than following notopodia), and ventral buccal cirri slightly longer than following ventral cirri. Third segment also with middorsal bulbous area. Parapodia subbiramous, notopodium small, on anterodorsal side of neuropodium, bluntly digitiform, with acicula, without notosetae; neuropodium larger, deeply cut dorsally and ventrally, with slightly longer, bluntly rounded presetal lobe, and shorter, bluntly rounded postsetal lobe. Neurosetae long, stout, with prominent subdistal swelling, well-developed basal semilunar pocket, rows of fine serrations, and strongly bidentate tips. Dorsal cirri on segments without elytra; cirrophores large, cylindrical, styles smooth, cylindrical basally, gently tapering distally; dorsal tubercles absent. Ventral cirri short, tapered. Nephridial papillae not present, pygidium with terminal anus and pair of anal cirri. Commensal on asteroid.

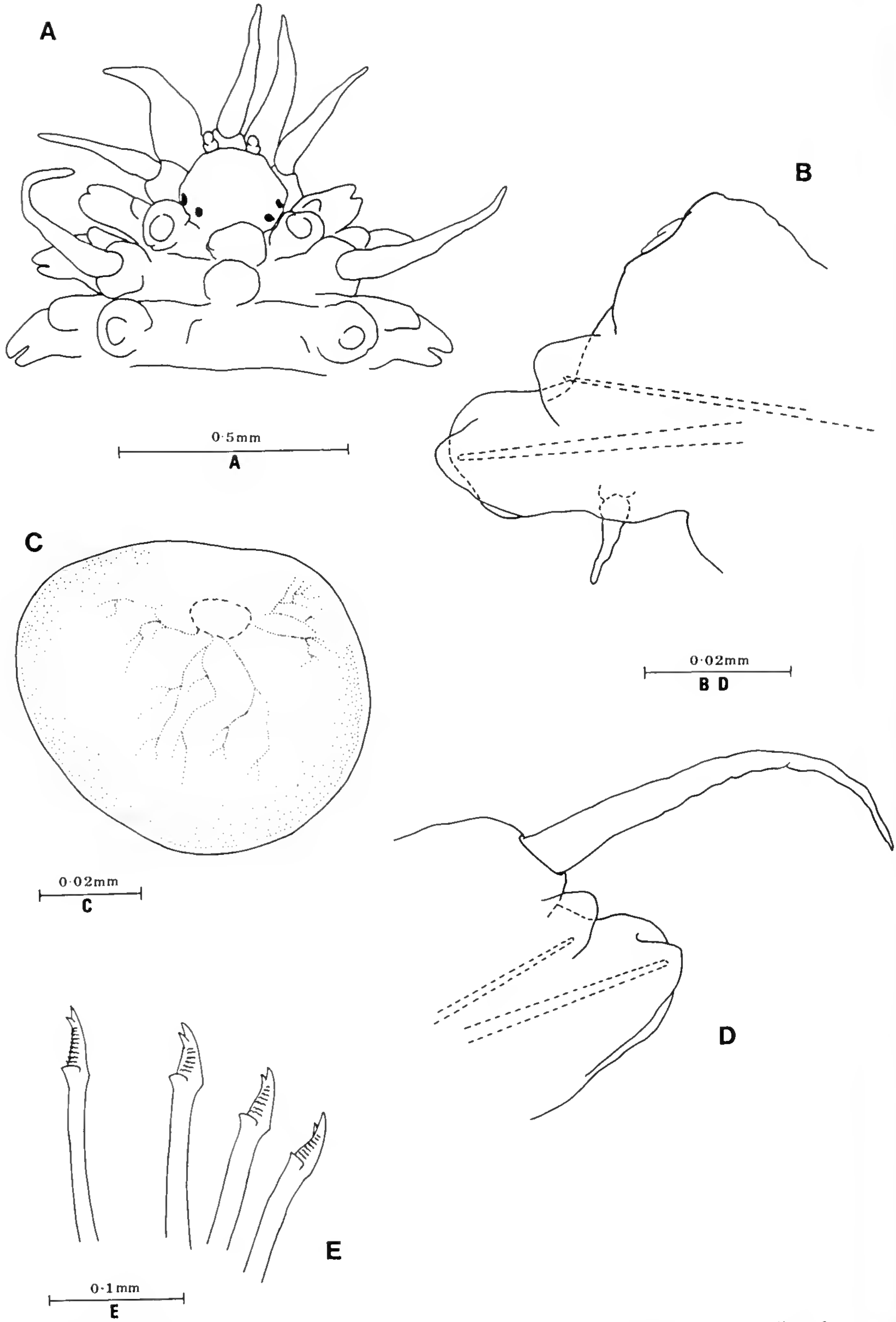

Fig. 1. *Capitulatinoe cupisetis* holotype: **A**, anterior end, dorsal view; **B**, elytragerous parapodium from posterior segment, anterior view; **C**, elytron from anterior segment; **D**, cirrigerous segment from anterior end, anterior view; **E**, neurosetae from anterior segment.

Etymology. The generic name *Capitulatinoe* refers to the relatively small prostomium of the type species.

Capitulatinoe cupisetis **sp.nov.**
(Figs 1A-E, 2A-D, 3A-E)

Type material. HOLOTYPE - NTM W2102, Mangrove Point, Broome, Western Australia, 17° 58.5'S 122° 14.5'E from ambulacral groove of asteroid, silt and sandy beach, 28.ix.1984 coll. R.Hanley. PARATYPES - NTM W2234, Mangrove Point, Broome, Western Australia 17°58.5'S 122°14.5'E, from ambulacral groove of asteroid, silt and sandy beach, 28.ix.1984 coll. R.Hanley. NTM W2173, Beach to right of caravan park, Mangrove Point, Broome, Western Australia 17°58.5'S 122°14.5'E, from ambulacral groove of asteroid, silt and sandy beach, 30.ix.1984 coll. R.Hanley.

Additional material. NTM W2323, Caravan park, Mangrove Point, Broome, Western Australia 17°58.5'S 122°14.5'E, from ambulacral groove of asteroid, silt and sandy beach, 1.x.1984 coll. R.Hanley. NTM W4383, W4384, W4386, W5354, W5355, Beach in front of Roebuck Bay, Broome, Western Australia 18°04'S 122°19'E, from ambulacral groove of asteroid, sandflat, 18.iii.1987 coll. R.Hanley, six specimens.

Description. *Holotype*: Body flattened, elongate, almost quadrate, flesh-coloured. Length 18mm, width including parapodia 1.3mm, 122 segments.

Elytra 77 pairs on segments 2, 4, 5, 7, alternate segments to 25, 26, 28, 29, 30, 32, 33, thereafter two elytragerous segments alternating with single cirrigerous segments to 59, 60, 61, then two elytragerous segments alternating with single cirrigerous segments to 102, 103, 104, 105, 106, 107, 108, 110, 111, 113, 114 and 116. Elytra large, soft, overlapping medially and posteriorly, covering dorsum. Elytra almost transparent, without tubercles or fringe of papillae, with faint band of dark pigment around border (Fig. 1C).

Prostomium roughly hexagonal, wider than long, truncate anteriorly, without cephalic peaks (Fig. 1A). Two pairs of eyes, anterior pair small, circular, lying dorsolaterally well behind widest part of prostomium, posterior pair slightly smaller, lying close behind anterior pair and closer to midline. Palps short, stout, tapered. Median antenna with large, cylindrical ceratophore inserted terminally on prostomium, with style smooth, basally cylindrical, tapering to fine tip; lateral antennae with very small, distinct ceratophores, inserted terminodorsally on prostomium above median ceratophore, styles very short, almost vestigial (Fig. 1A). Tentacular segment not visible dorsally, tentaculophores of moderate length, lateral and ventral to prostomium, achaetous, with two pairs of smooth dorsal and ventral tentacular cirri, dorsal pair similar in length and shape to median antenna, ventral pair much shorter. Facial tubercle absent.

Segment 2 with middorsal bulbous area (Fig. 1A), first pair of large elytrophores, subbiramous parapodia (notopodium much smaller than notopodia of following segments), and ventral buccal cirri only slightly larger than following ventral cirri.

Segment 3 with middorsal bulbous area (Fig. 1A).

Parapodia subbiramous (Fig. 1B,D). Notopodium small, bluntly digitiform, on anterodorsal side of larger neuropodium, with notoacicula, without notosetae. Neuropodium (Fig. 1B,D), deeply cut dorsally and ventrally, with slightly longer, rounded presetal acicular lobe and shorter bluntly rounded postsetal lobe.

Neurosetae few, very stout, curved, with subdistal swelling, conspicuous semilunar pocket, several rows of fine serrations, and hooked, strongly bidentate tips (Fig. 1E). Upper neurosetae slightly thinner and straighter than lower ones.

Dorsal cirri on segments without elytra, with large, cylindrical cirrophores; styles basally stout, tapering gradually to tips (Fig. 1D). Dorsal tubercles absent. Ventral cirri short, subulate. Nephridial papillae not visible. Ventrum swollen.

Pygidium small, terminal, with pair of anal cirri similar to dorsal cirri.

Commensal on the starfish *Astropecten granulatus* Müller and Troschel, 1842.

Paratypes: Two specimens, NTM W2173 is 20mm long and 1.2mm wide, including parapodia with 116 segments and 75 pairs of elytra; NTM W2234 is 41 mm long and 1.7mm wide, including parapodia with 181 segments and more than 100 pairs of elytra.

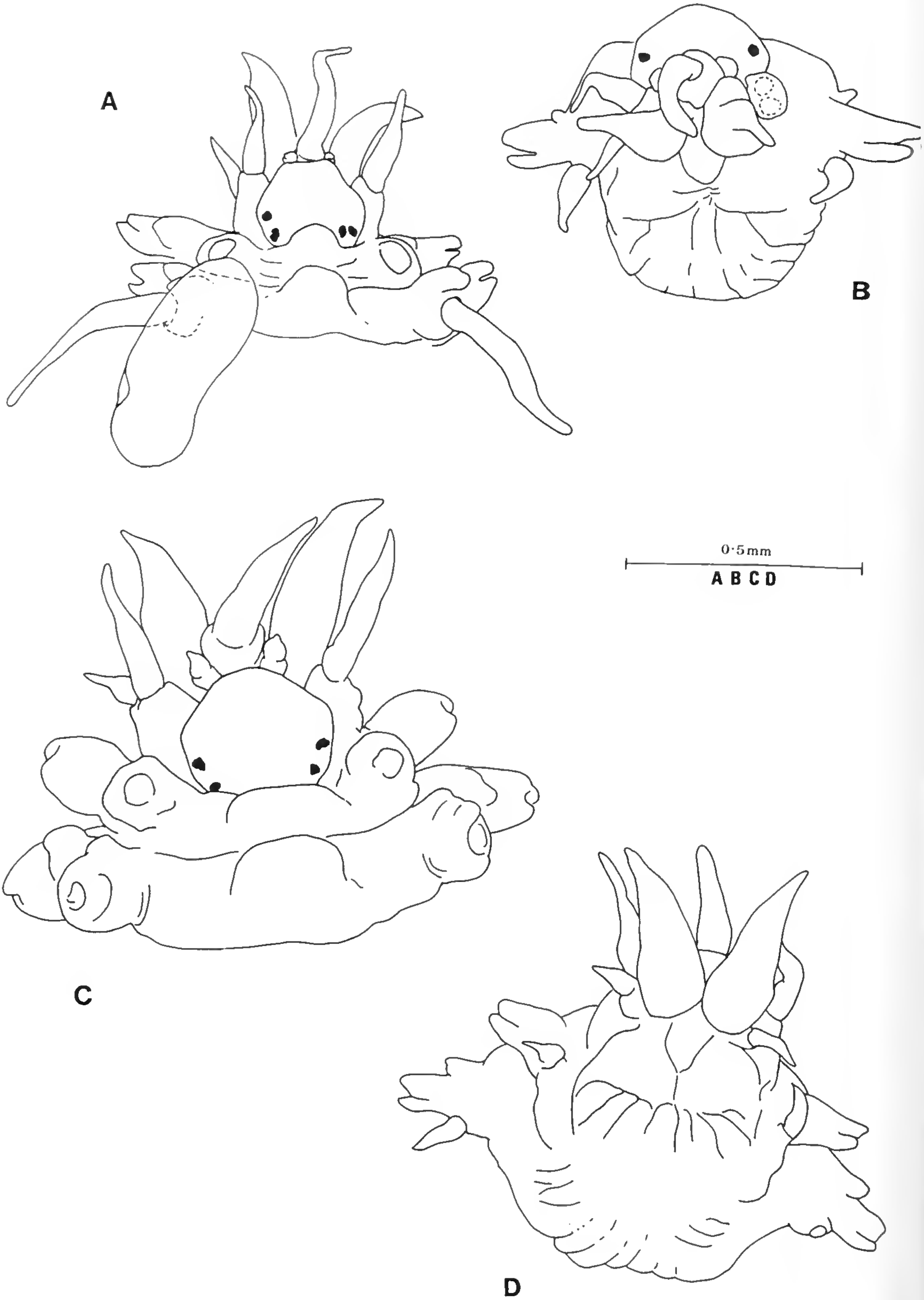

Fig. 2. *Capitulatinoe cupisetis*: **A**, anterior end, NTM W4384; **B**, frontal view of anterior end, NTM W4384; **C**, anterior end, paratype, NTM W2234; **D**, ventral view of anterior end, NTM W4384.

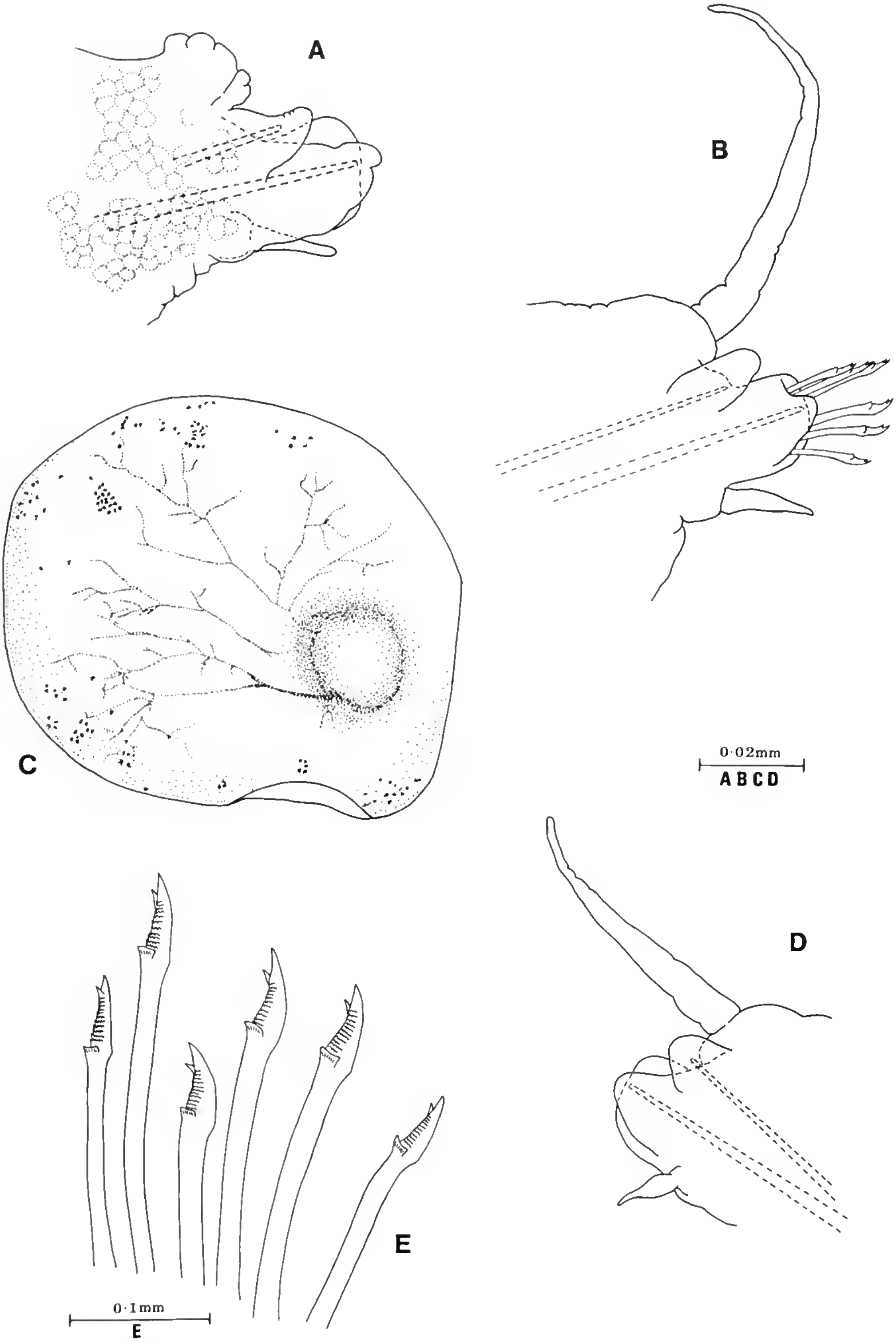

Fig. 3. *Capitulatinoe cupisetis*: **A,** elytragerous parapodium from middle segment, anterior view, NTM W5355; **B,** left cirrigerous parapodium from 18th segment, anterior view, NTM W4384; **C,** right elytron from posterior segment, NTM W5355; **D,** anterior view of cirrigerous parapodium from anterior segment, paratype, NTM W2173; **E,** neurosetae from anterior segment.

The two paratypes are very similar to the holotype in shape of prostomium, antennae, and parapodia. The neurosetae are also similar.

The elytra of both paratypes and those of the additional material are arranged in the same pattern on the anterior part of the body. Up to segment 33, the arrangement on all the material examined here shows the same pattern as that recorded for the holotype, thereafter, on all material the basic pattern of attachment is for two elytragerous segments to alternate with single cirrigerous segments. However, on most of the specimens examined there is some departure from this arrangement with up to six elytragerous segments between cirrigerous segments on the posterior end of the body.

Most of the additional specimens are incomplete, missing either heads or posterior ends. There is good general agreement between these fragments and the type material in respect of characteristics of prostomium (where present), parapodia, setae, elytron attachment pattern, and ornamentation of elytra (Figs 2A-D, 3A-E).

Habitat. Commensal in the ambulacral grooves of the starfish *Astropecten granulatus*.

Distribution. Known only from the type locality, Broome, Western Australia.

Etymology. The species name *cupisetis* refers to the presence of cuplike (semilunar) pockets on the neurosetae.

Remarks. The presence of semilunar pockets on the neurosetae of this species places it close to the other polynoid genera which also have semilunar pockets, reviewed by Pettibone (1969). The new genus differs from the four other genera in several important respects and these are compared in Table 1.

Subadyte Pettibone, 1969 and *Paradyte* Pettibone, 1969 are easily distinguished from the new genus because they are short bodied forms with a fixed number of pairs of elytra (Table 1).

The other two genera are both long bodied forms like the new genus *Capitulatinoe*. However, *Adyte* Saint Joseph, 1899, *sensu* Pettibone 1969, has only 15 pairs of elytra.

Pottsiscalisetosus is clearly the closest to *Capitulatinoe*. Both genera are long bodied with numerous pairs of elytra; have a middorsal bulbous area on segment 2, similar parapodial features, and are commensal on starfishes.

There are several features which distinguish these two genera. The ceratophores of

Table 1. Comparison of major characters between genera with semilunar pockets on the neurosetae (compiled from Pettibone 1969).

Genus	Pairs of elytra	Elytra attached to segment No.	Notosetae	Neurosetae	Other
Adyte Saint Joseph, 1899; emend. Pettibone 1969	15	2,4,5,7, alternate segments to 23,26,29 & 32	nearly smooth with scattered, closely opposed spinous rows.	faint rows of serrations, minutely bifid, hooked tips.	North Atlantic, North Sea, Mediterranean, commensal with echinoids
Subadyte Pettibone, 1969	15 or 16	2,4,5,7 alternate segments to 23, 26, 29, 32 and sometimes 34	spinous pouches along convex edge.	rows of spinous pouches, tips hooked, bifid.	Atlantic, Indian, and Pacific Oceans, Mediterranean, several species commensal on echinoids and ophuiroids, others free-living.
Paradyte Pettibone, 1969	15	2,4,5,7, alternate segments to 23,26,29 and 32	few spines along convex edge.	two kinds: supra-acicular slender, elongate spinous regions and slightly hooked bifid tips; subacicular much shorter with short falcate smooth tips.	Indo-West Pacific, one species commensal on crinoids, other species hosts uncertain.
Pottsiscalisetosus Pettibone, 1965	numerous	2,4,5,7, alternate segments to 23,26,29, 32,33,35 continuing on alternate segments to end of body (sometimes irregular after segment 39).	finely serated	slightly to distinctly hooked, finely serrated.	Japan, Ceylon, commensal with asteroids.
Capitulatinoe n. gen.	numerous	2,4,5,7, alternate segments to 25,26,28, 29,30 then two elytragerous segments alternate with single cirrigerous segments to end of body (usually some irregularity posteriorly).	absent	slightly to distinctly hooked, finely serrated, strongly bifid.	Broome, Western Australia, commensal with asteroids.

the lateral antennae on *Capitulatinoe* are inserted on a slightly higher level than the ceratophore of the median antenna, while on *Pottsiscalisetosus*, the ceratophores of the lateral antennae are inserted terminoventrally, slightly ventral to the ceratophore of the median antenna (see Fig. 9a in Pettibone 1969). In addition to the middorsal bulbous area on segment 2, there is a slightly smaller bulbous area on segment 3 on *Capitulatinoe*. *Pottsicalisetosus* has notosetae, these are lacking on *Capitulatinoe*. The elytral arrangement on the anterior part of the body form segment 23 differs on the two genera and, while both genera show some variability posteriorly, the basic pattern differs (Table 1).

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A DESCRIPTION OF HORNED-TURTLE REMAINS (TESTUDINES:MEIOLANIIDAE) FROM THE MID-MIOCENE CAMFIELD BEDS OF NORTHERN AUSTRALIA

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ABSTRACT

New horned-turtle fossil material from the mid- to late-Miocene Bullock Creek Local Fauna (Camfield Beds) of the Northern Territory of Australia is referrable to the genus *Meiolania* on the basis of its morphological similarity to the Pleistocene-aged *Meiolania platyceps* Owen from Lord Howe Island. A single individual is represented by cranial fragments, and second and fifth cervical vertebrae. In some details, the Bullock Creek *Meiolania* more closely resembles fragmentary material from New Caledonia, some of which has been assigned to a poorly defined taxon, *M. mackayi* Anderson. A species determination for the Bullock Creek *Meiolania* is not yet possible. The possible relationships of the New Caledonian and other undetermined Australian mid-Tertiary meiolaniids to *M. platyceps* are briefly discussed.

KEYWORDS: Horned turtle, fossil, Miocene, Camfield Beds, Australia, *Meiolania*.

INTRODUCTION

The Meiolaniidae are a most unusual, extinct family of large turtles from the Cainozoic of South America, Australia and several western Pacific islands. Meiolaniid skulls are elaborated by horns, frills and bosses, the cervical vertebrae bear ribs, and the tail is sheathed distally by a club. Owen's (1881) description of meiolaniid remains, mistakenly referred by him to the giant Pleistocene varanid, *Megalania* Owen, marked the beginning of more than a century of scientific publications on the group. Late nineteenth century confusion about the place of meiolaniids within the Reptilia and the subsequent controversy over whether they belonged with the cryptodiran or the pluerodiran turtles has been well recounted by Gaffney (1983) and this work is an excellent introduction to the earlier literature. On the basis of shared, derived skull characters, Gaffney (1975) places the Meiolaniidae with the Cryptodira. Further discussion of the phylogeny of the group at higher taxonomic levels is included in Gaffney (1983,1985).

In 1985 and 1986 members of the Northern Territory Museum's palaeontological expeditions to Camfield Station collected fragmentary remains of a meiolaniid from the mid- to late-Miocene Camfield Beds. Meiolaniid fossils have previously been reported from the mid-Tertiary of Australia (Etheridge 1889; Gaffney 1981) so their presence in the Camfield Beds was not entirely unexpected. The Bullock Creek meiolaniid shows a general morphological similarity to the Pleistocene *Meiolania platyceps* Owen (1886) from Lord Howe Island, although in some details it more closely resembles fragmentary material, also Pleistocene-aged or younger, from New Caledonia described by Anderson (1925) and Gaffney *et al.* (1984). Some New Caledonian material was assigned to a poorly defined species, *Meiolania mackayi* Anderson (1925), a taxon close to *M. platyceps*. The Bullock Creek form is referrable to the genus *Meiolania*, but a species determination is not yet possible. A description of the new material may be useful in future taxonomic studies.

The only other Australasian taxon, *"Meiolania" oweni* (Woodward, 1888) from the Pleistocene of Queensland and New South Wales, is clearly more closely related to the

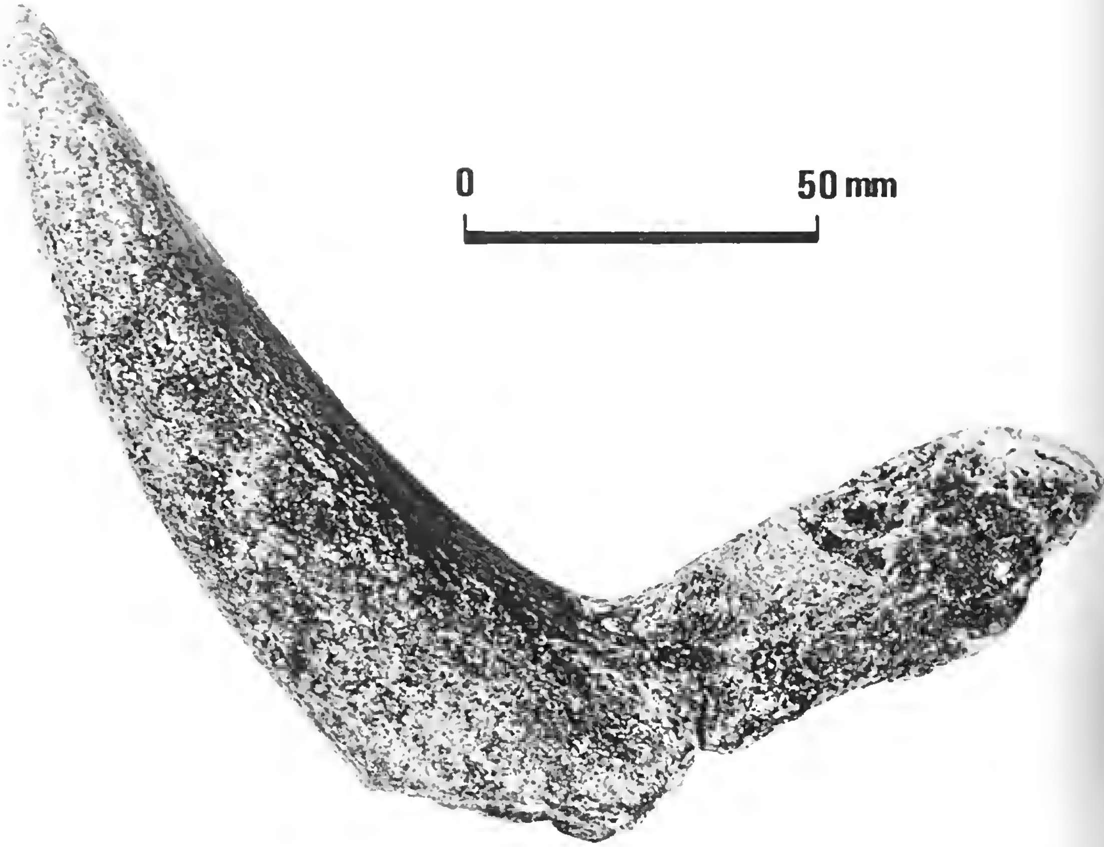

Fig. 1. Bullock Creek *Meiolania* right squamosal fragment NTM P87103-2 in dorsal view. Posterior is towards the top of the page.

two Argentinian forms, *Niolamia argentina* Ameghino, 1899 from the pre-Oligocene, and *Crossochelys corniger* Simpson, 1937 from the Eocene. A reappraisal of this lineage, with its confusing literature (see Gaffney 1983:393), is in preparation by Gaffney. Useful descriptive references for these taxa are; Owen (1881) for *"Meiolania" oweni*, Woodward (1901) for *Niolamia argentina*, and Simpson (1938) for *Crossochelys corniger*. Simpson (1938) also provides useful comparisons, revised in some details by Gaffney (1983). Gaffney (1981) reviewed the then known Australian/Pacific island meiolaniid fossils, including undetermined material, and summarised principal differences between all the known forms.

Comparisons presented here are with published descriptions. Prefixes to catalogue numbers are as follows : AM Australian Museum, Sydney; MM Mining and Geological Museum, Sydney; NCP, NCT Muséum National d'Histoire Naturelle, Paris; NTM Northern Territory Museum, Darwin.

STRATIGRAPHIC PALAEONTOLOGY

The Bullock Creek Meiolania was recovered from the Camfield Beds at a location described by Plane and Gatehouse (1968) as "16 miles southeast of Camfield Homestead in the north central Northern Territory" (approximate latitude 17°S, longitude 131°30'E). The Camfield Beds are fluvial and lacustrine calcareous conglomerates, sandstones and siltstones, with basal ferruginisation and silicification on top. No suitable techniques are yet avaliable to establish the absolute age of the Camfield Beds, but on the basis of the stage-of-evolution of marsupial components of the Bullock Creek Local Fauna, a mid- to late-Miocene age is estimated. Woodburne *et al.* (1985) provide the most recent review of the biochronology of

Australian Tertiary vertebrate-fossil deposits and outline the methodologies used for estimating their ages.

SYSTEMATICS

Material. All the specimens listed below were collected from within a few metres of each other at a locality known informally as the "Blast Site". Their juxtaposition, preservation and respective sizes suggest that a single individual is represented. The fossils were extracted from their limestone matrix using acetic acid. Carapace and plastron fragments, and a dermal ossicle, were also recovered, but are not described here. They do not appear to differ in any noteworthy respect from *M. platyceps*.

NTM P87103-2, right squamosal fragment bearing a cow-like horn; NTM P87103-3, left squamosal fragment with the horn sheared off, but part of the cavum tympani preserved; NTM P8695-93, second cervical (axis) vertebra lacking right parapophysis; NTM P87103-4, fifth cervical vertebra lacking right parapophysis.

Description. Gaffney (1983) provides a detailed description of the cranial morphology of *M. platyceps*, and his terminology for cranial scale (scute) areas and the osseous excrescences encompassed by them is followed here.

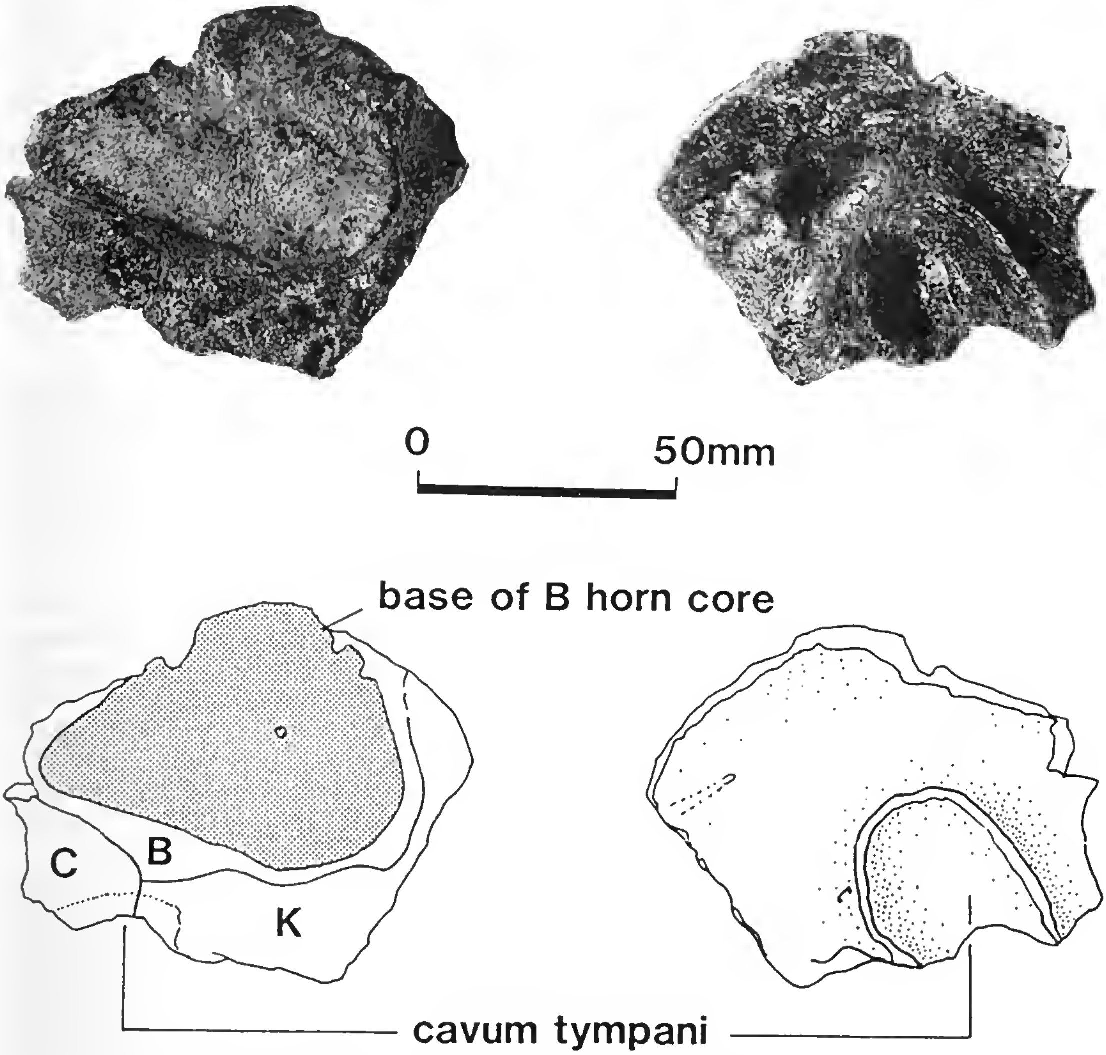

Fig. 2. Bullock Creek *Meiolania* left squamosal fragment NTM P87103-3 in (a) left lateral and (b) internal views. The designation of epidermal scute areas (B, C and K) follows the system of Gaffney (1983).

NTM P87103-2 (Fig. 1) and NTM P87103-3 (Fig. 2) are composed wholly of right and left squamosal respectively; no osseous sutures are discernable on either fragment. The cavum tympani, partially preserved with NTM P87103-3 (Fig. 2), shows a close correspondence to the examples of *M. platyceps* (AM F16866) and *M. mackayi* illustrated in Anderson (1925, Plate 32, Figs 4 and 6 respectively).

On both Bullock Creek cranial fragments the B scute margins are clearly defined by shallow sulci, but others are less certain, partly because of their short truncation by the broken edges of the fragments. The interpreted scute patterns (Fig. 2 and Fig. 3) do not appear to differ from *M. platyceps*. In *M. platyceps*, perhaps uniquely within the Testudines, epidermal sutures are marked on the skull by low ridges (Anderson 1925; Gaffney 1983).

The cowlike B horn core preserved with NTM P87103-2 projects from the posterolateral skull margin. Its angle of projection, when viewed from the lateral or medial sides, is towards the posterior with little dorsal rise. The horn core is long, slender and terminates acutely. In any profile it is smoothly curved.

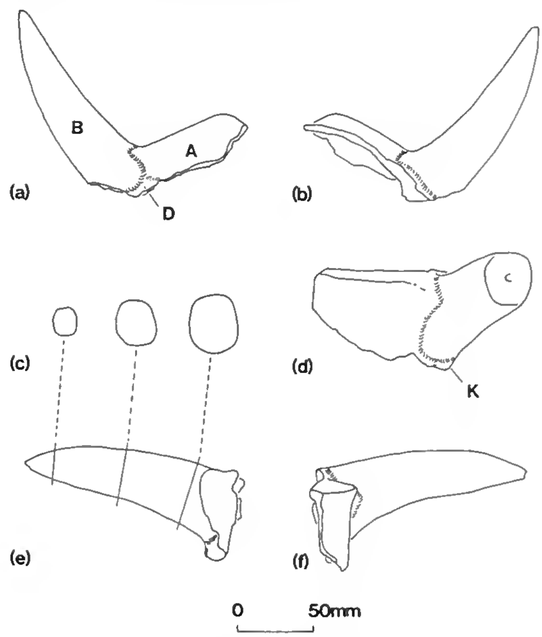

Fig. 3. Bullock Creek *Meiolania* horn-bearing cranial fragment, NTM P87103-2: (a) dorsal view; (b) ventral view; (c) transverse sections of the B horn core; (d) posterior view; (e) right lateral view; (f) medial view. The designation of epidermal scute areas (A, B, D and K) follows the system of Gaffney (1983).

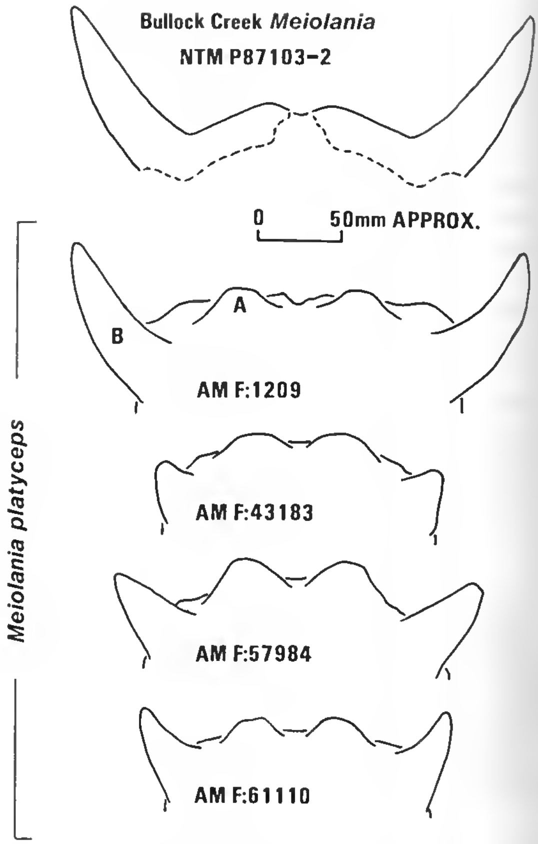

Fig. 4. Partially restored posterior skull region of the Bullock Creek *Meiolania* compared with examples of *M. platyceps*. The *M. platyceps* examples, after Gaffney (1983: Fig. 22, AM F57984; Fig. 24, AM F1209; Fig. 38, AM F43183; Fig. 40, AM F61110), show the extremes of development in the B horn cores (AM F1209, largest; AM F43183, smallest) and the A horn cores (AM F57984, largest; AM F61110, smallest).

The dorsal, ventral, lateral and medial sides are flattened so that the transverse section at any point along the length resembles a rounded rectangle whose longest sides are aligned dorsoventrally. On the medial side there is a shallow, longitudinal sulcus, restricted to the mid one-third of the length. The horn core surface is sculptured by nutrient foramina and canals.

The Bullock Creek B horn core is longer and more slender than any recorded example of *M. platyceps*. The ratio of the width at the base (estimated after restoration of the sheared-off portion) to the length, measured from the bone surface on the inside of the skull to the tip, is 0.32. This is outside the range (>0.40, <0.90) given for a sample of 50 *M. platyceps* B horn cores (Gaffney 1983).

In proportions it more closely resembles the *M. mackayi* B horn core (Anderson 1925, Plate 32, Fig. 5).

M. platyceps has a pair of short, dorsoventrally-flattened A horn cores which project posterodorsally from the posterodorsal skull margin. This pair show a lesser degree of morphological variability than the B horn cores, and their size in any individual does not appear to be related to the degree of development of the B horn core (Gaffney 1983). On NTM P87103-2 the comparable region of the skull is slightly thickened in the posterior direction, but is not expanded into a foundation for a cranial horn (Fig. 4).

The Bullock Creek second cervical vertebra NTM P8695-93 (Fig. 5) is shorter anteroposteriorly, laterally compressed and dorsoventrally extended when compared with that of *M. platyceps* (Fig. 6). The lateral compression is reflected in the higher than wide central articulations and the shorter diapophyses (transverse processes). The neural spine is a broad, massive structure, rising high over the zygapophyses before arching anteroventrally and flaring laterally to an elevated position over the prezygapophyses. The ventral surface of the elevated part of the neural process has two, deep, oval fossae, separated by a medial keel, which may have provided for the deep insertion of rectus capitus muscles. In *M. platyceps* "the neural arch of the second cervical virtually lacks a neural spine, instead it is a broad, flat platform, that seems to articulate with the underside of the skull roof" (Gaffney 1985:7). The neural process of the Bullock Creek cervical does have a flattened area, roughly diamond-shaped in dorsal view and somewhat smoother than the more rugose adjacent parts, which may represent that portion of the spine normally in articulation with the skull.

Other morphological features of the Bullock Creek second cervical conform with those of *M. platyceps*. The centrum is opisthocoelous. Fused to the dorsoventral centrum margins were paired intercentra (Gaffney 1985), represented only on the left side of NTM P8695-93 by the posterolaterally-projecting parapophysis. Its small, terminal, parapophyseal articular facet marks the point of attachment for the ventral head (capitulum) of the third cervical rib. The dorsal head (tuberculum) of the second cervical rib articulated over a relatively large surface at

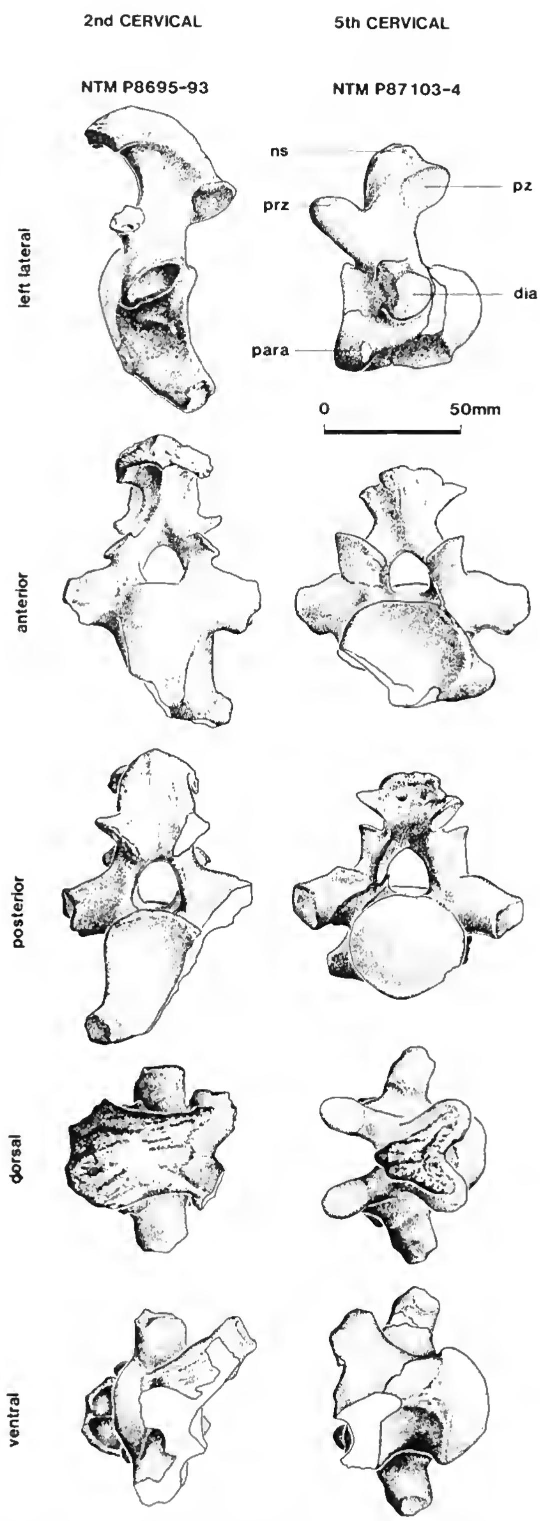

Fig. 5. Bullock Creek *Meiolania* second cervical vertebra NTM P8695-93 and fifth cervical NTM P87103-4. Abbreviations: **dia**, diapophysis; **ns**, neural spine; **para**, parapophysis; **prz**, prezygapophysis; **pz**, postzygapophysis.

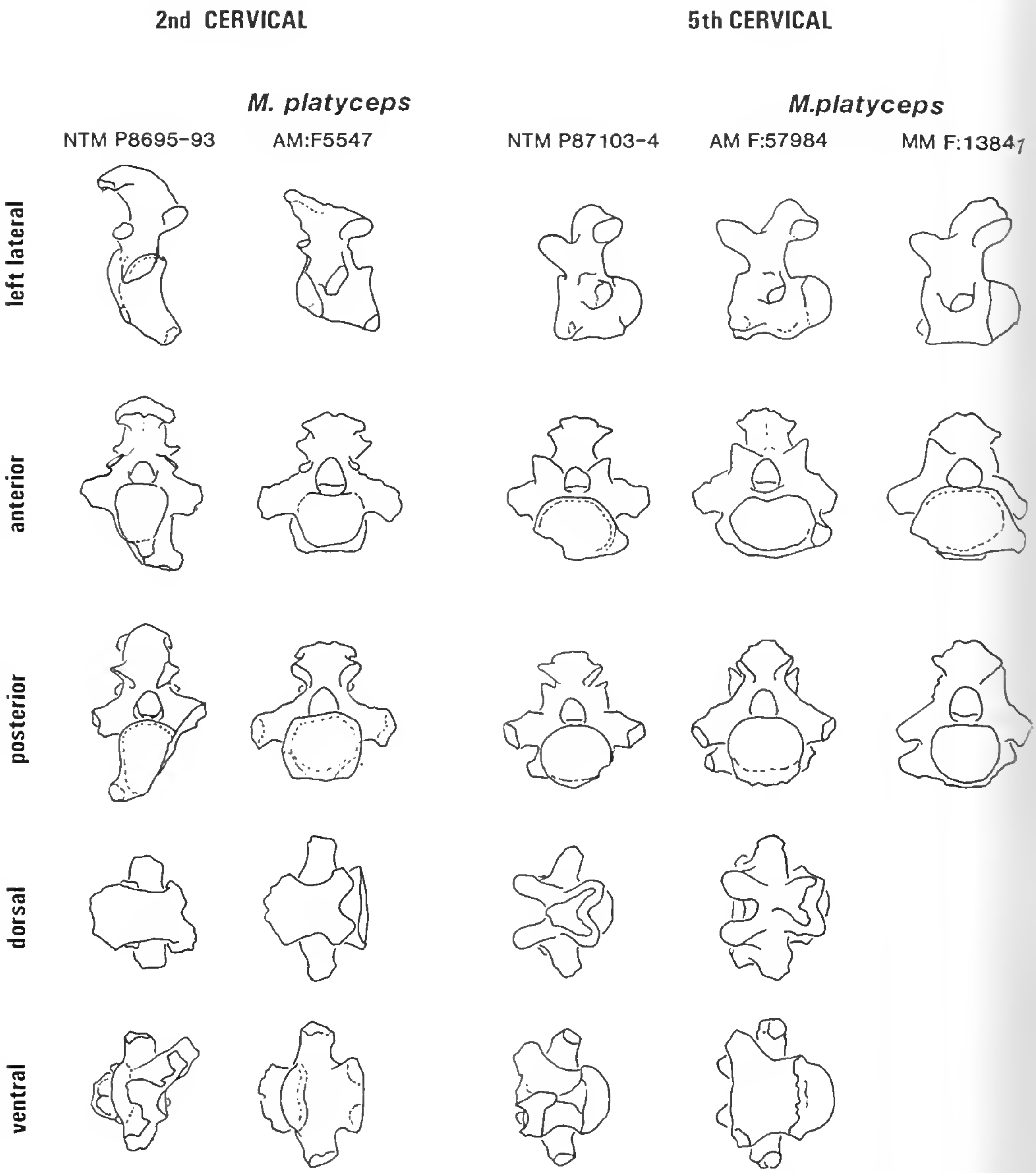

Fig. 6. Bullock Creek *Meiolania* cervicals compared with examples of *M. platyceps*. AM F: 5547 and AM F:57984 after Gaffney (1985, Fig. 5), MM F: 13847 after Owen (1888, Plate 35, Figs 1-3).

the end of the robust diapophysis, which emerges partly from the neural arch and partly from the vertebra centrum. The cervical ribs of *M. platyceps* and their mode of attachment are described in detail by Gaffney (1985).

The prezygapophyses are borne on short anterior projections of the neural arch, emerging at about mid-level of the neural canal. Their articular facets are small and face dorsolaterally. The ventrolaterally-facing postzygapophyseal articular surfaces are relatively large and are situated high on the neural arch, entirely above the level of the neural canal.

The Bullock Creek fifth cervical vertebra, NTM P87103-4, (Fig. 5) differs from *M. platyceps* in having a more upright neural spine and a keeled centrum (Fig. 6). The keel was intercepted by the rock drill during collection, but is complete enough for restoration. In *M. platyceps* the fifth cervical has indistinct, low, parasaggital ventral ridges (Gaffney 1985).

Proportionally, NTM P87103-4 falls within the range for *M. platyceps*, and apart from the features listed above, is morphologically similar. The centrum is procoelous; the anterior central articulation is deeply concave, and the posterior one, bulbous. The preserved left parapophysis is attached anterolaterally and has a small, posterolaterally-facing articular facet. The diapophyses, projecting laterally from midway along the centrum length at the contact of the neural arch and the centrum, have lárge, posterolaterally-facing articular surfaces. Both the prezygapophyses and postzygapophyses are widely separated and situated high on the neural arch. Their articular surfaces are relatively large and all are of a similar size. The prezygapophyseal articular surfaces face dorsomedially, while the postzygapophyseal articular surfaces face ventrolaterally. As in *M. platyceps* the neural spine is a low, blunt swelling.

DISCUSSION AND SYSTEMATIC DETERMINATION

Radiation within the Meiolaniidae is poorly understood with only *M. platyceps* well represented by fossil material. The cow-like B horn core and the absence of any osseous, posterodorsal cranial frill aligns the Bullock Creek horned turtle with *Meiolania platyceps* and *M. mackayi* and separates it from *"Meiolania" oweni*, *Niolamia argentina* and *Crossochelys corniger*. The Bullock Creek material is considerably older than the Pleistocene *M. platyceps* and *M. mackayi* but the geological range of meiolaniid taxa are as yet unknown. The general morphological similarity of the Bullock meiolaniid to *M. platyceps* justifies its assignment to the genus *Meiolania*, but a specific determination awaits the recovery of additional diagnostic material.

The distinctive features of the Bullock Creek meiolaniid, possibly of some taxonomic significance are, relative to *M. platyceps*: the long, slender, cow-like , B horn core projecting at a low angle; the absence of paired A horn cores; the short, laterally compressed, and dorsoventrally extended second cervical vertebra; and the keeled fifth cervical. The presence of some comparable features in other fragmentary material is intriguing.

Anderson (1925) distinguished *M. mackayi* from Walpole Island (New Caledonia) from *M. platyceps* by its smaller size and more slender cranial horn. The Bullock Creek cranial horn is relatively slender, and in this respect resembles *M. mackayi*. Anderson (1925) commented on the variability in the shape and size of the *M. playtceps* cow-like cranial horn and noted that a sufficiently large sample of *M. mackayi* might overlap with *M. platyceps*. *M. mackayi* remains poorly defined, the cervical vertebrae are unknown, and other postcranial elements differ from *M. platyceps* in size only.

Gaffney *et al.* (1984) describe two cervical vertebrae from New Caledonia. The Tiga Island centrum (NCT 01), probably of a seventh cervical, corresponds closely with *M. platyceps* examples from Lord Howe Island, but the complete Pindai Cave seventh cervical (NCP 05) retains a number of distinctive features. It differs from Lord Howe Island *M. platyceps* in having almost round (rather than laterally elongate) central articulations, a well-developed ventral ridge (keel) and no indication of broad sutural contact for the parapophyses. Gaffney *et al.* (1984) suggest that these three characters may be of some taxonomic significance, but were not able to assign the vertebrae to any meiolaniid taxon. Unfortunately, no seventh cervical from Bullock Creek has yet been recovered, but the laterally compressed second cervical with its higher than wide central articulations, and the keeled fifth cervical, are suggestive, particularly if the sequential variation in the *M. platyceps* cervical series (Gaffney 1985) is used as a guide.

Also worthy of mention here is an unassociated, unusually short, atlantal neural arch from Lord Howe Island (AMF:18835) described by Gaffney (1985). Its degree of shortening relative to other examples from Lord Howe Island parallels the relative shortness of NTM P8695-93 compared with *M. platyceps* axis vertebrae. Gaffney (1985) commented that "..AM F18835 is not so easily interpreted as individual variation",

but left it as an aberrant example of *M. platyceps*.

Etheridge (1989) described a ?Miocene (see Gaffney 1981:28; Woodburne *et al.* 1985) meiolaniid from Gulgong, New South Wales. Gaffney (1981:29) regards it as "a taxon allied to *Meiolania platyceps* because of the 'cow-like' cranial horn but differing from the Lord Howe Island species in the low and thin shape of the horn" and noted that the lower jaw and tail club fragments also differed. The Gulgong B horn core is much smaller than the one from Bullock Creek, though this feature may be attributable to individual variation if *M. platyceps* is any guide. A cervical vertebra mentioned in a footnote by Etheridge (1889) has not been described.

Remains of a *M. platyceps*-sized meiolaniid have also been recovered from mid-Miocene (Woodburne *et al.* 1985) sediments at Lakes Pinpa, Ngapakaldi and Pitikanta, South Australia. Manus elements are nearly identical to those of *M. platyceps* (Gaffney 1981:24). Apart from a plastron fragment, none of the material listed by Gaffney (1981) overlaps with Bullock Creek specimens currently avaliable.

The relationship of various forms apparently allied to *M. platyceps* cannot yet be convincingly demonstrated, but the possibilities bear brief mention. The distinctive features preserved with the fragmentary material listed above may simply represent temporal and geographic variants of an unbranching meiolaniid lineage culminating in *M. platyceps*. Thus, the Lord Howe Island *M. platyceps* could be derived directly from the Bullock Creek *Meiolania* by the development of A horn cores, loss or reduction of a ventral keel in the posterior cervicals, and some changes in proportions. Alternatively, these character states may indicate a radiation, with some members of the genus *Meiolania* as sister taxa. One possibility has *Meiolania platyceps* and the Bullock Creek *Meiolania* sharing a common ancestor, with descendants of the Bullock Creek form persisting into the Pleistocene or Recent of New Caledonia. An alternative theory of radiation involves a split in post Bullock Creek times, with the appearance of derived features in the *M. platyceps* lineage, and retention of a more plesiomorphic character complex in a New Caledonian form.

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THE CRANIUM OF *HADRONOMUS PUCKRIDGI* WOODBURNE, 1967 (MACROPODOIDEA: MACROPODIDAE) A PRIMITIVE MACROPODID KANGAROO FROM THE LATE MIOCENE ALCOOTA FAUNA OF THE NORTHERN TERRITORY

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ABSTRACT

Originally described from its dentition and lower jaw only, the affinity of *Hadronomus* within the Macropodidae had not been resolved. The cranium of *Hadronomus* gives a better understanding of its broader affinity with other kangaroos, although its precise systematic position remains ambiguous with regard to known fossil and living macropodids. On the basis of its cranial wall morphology and its previously described dentition, *Hadronomus* appears to be a member of the Macropodidae that shares predominately plesiomorphic features with the sthenurines. Otherwise, *Hadronomus* is very distinctive in many respects from known macropodines and sthenurines, and it has not been possible to establish a direct relationship with any named annectant macropodid group. The maxilla and molars of an unassigned mid-Miocene form described by Flannery *et al.* (1982) resemble those of *Hadronomus*, as do some specific features of the lower molars, dentary and incisor of *Galanarla tessellata*, another primitive macropodid of unknown subfamilial affinity. The genus *Hadronomus* appears to be the terminal form of an ancient lineage of macropodids that could represent a sister group of the Sthenurinae.

KEYWORDS: Macropodid cranial morphology, Sthenurinae, late Miocene, macropodid systematics.

INTRODUCTION

Woodburne (1967) concluded from the dentition that *Hadronomus* shows a number of characters "...which are prophetic of Pliocene and Pleistocene protemnodonts and ... late Cenozoic members of the Sthenurinae. Because the late Cenozoic history of the Macropodidae is poorly understood and because temporally and structurally intermediate forms are absent, the animal cannot be assigned to a subfamily." A significant further observation was that considerable morphological change would have had to occur if *Hadronomus* were ancestral to *Sthenurus* and/or *Protemnodon* and finally, that *Hadronomus* "...is better suited as an ancestor to *Sthenurus* than to *Protemnodon*."

While the possible relationships of *Hadronomus* to subsequent later Cenozoic macropodine genera are of great interest, little can be added to Woodburne's observations based on the dentitions. Some features of the cranium of *Hadronomus* appear to support his opinion that the genus is closer to *Sthenurus* than to *Protemnodon*. On the other hand, *Hadronomus* has many unique characters and character combinations that may have some bearing on the broader question of macropodid-potoroid relationships.

The dentition of *Hadronomus* has been described in detail by Woodburne (1967) and requires no further treatment at this time. Although dentitions of *Hadronomus* are relatively common in the Alcoota Fauna, even fragmentary remains of the cranium are extremely rare. The specimen in this description (NT Museum number ASP889) was recovered during the last few days of our 1988 field season. The context of the specimen was unusual in being found isolated from the typical bone-bed material. The cranium was preserved in poorly consolidated sediment, lying adjacent to the cranium of a pouch

young of *Kolopsis torus*. No other significant remains were recovered from the immediate area.

MATERIALS AND METHODS

ASP889 (*Hadronomus puckridgi*) a partial cranium including right maxilla, palate, jugal, auditory region and a portion of the orbital wall and neurocranium. The dorsal surface of the neurocranium and rostrom is missing, as is most of the premaxilla and its dentition. The specimen is slightly compressed dorsoventrally. The cranium was directly compared with whole and dissected cranial specimens of the extant forms *Aeypyprymnus rufescens, Potorous tridactylus, Onychogalea unguifera, Thylogale billardieri*, and *Macropus* spp.

SYSTEMATICS

The classification of *Hadronomus puckridgi* Woodburne, 1967 follows Aplin and Archer (1987), as follows: Suborder Phalangerida, Superfamily Macropodoidea, Family Macropodidae, Subfamily *Incertae sedis.*

Aplin and Archer (1987) argue for the separation of the Potoroidae and Macropodidae at the familial level. They base their conclusions on the gross morphological differences in female reproductive tracts and spermatozoan morphology of the respective families. They also suggest that there is both biochemical and palaeontological evidence of an early separation of the two families "...perhaps sometime during the Oligocene" (Aplin and Archer 1987). I support Aplin and Archer's conclusion, if not all of their reasoning, because of the enormous sometimes radical diversification within both divisions and the anomalous results of implying equivalent morphological distance between say, the Sthenurinae and the Macropodinae and the Potoroniae and the Macropodinae.

Subfamily *Incertae*
(Figs 1-7)

Hadronomus puckridgi Woodburne, 1967:82-103, figs 14-17.

Revised diagnosis. Low, broad neurocranium with alisphenoid-parietal contact; widest at the level of the glenoid fossae. Zygomatic arch long, straight; jugal strap-like and deep throughout its entire length. Lateral glenoid eminence highly developed. Poorly developed prezygomatic sulcus and short, blunt masseteric processes. Orbital margin thin, sharp; small, deep, elliptical orbital fossa. Masseteric crest on jugal straight, attachment surface of the masseter not expanded anteroventrally towards the masseteric process. Palate with large, posteriorly confluent greater palatine vacuities; diastemal and premaxillary palate, not strongly flexed downwards; shallow, posteriorly tapering suborbital shelf. Low, elongated auditory arch, strongly slanted posteriorly; wide, ventrally thick, cancellous, posterodorsally incomplete ectotympanic, large elliptical auditory meatus. Alisphenoid tympanic wing relatively broad and slightly inflated. Petrous bone elongated, floccular fossa large, oval in outline and shallow with rounded orificial margins. Posterior neurocranium low relative to the occlusal line. Upper cheektooth row slightly curved, upper permanent premolar elongated, sectorial; shearing crest consisting of seven small cusps and bearing a low lingual crest. Upper molars low crowned, simple, bilophodont and lacking ornamentation, lophs thin and trenchant; crowns lengthen anterior to posterior, broad midvalleys widen progressively from front to back, blocked labially by two longitudinal crests (buccal cingulum and postparaconal crest) divided by a sulcus. M_2 with low, wide short anterior midlink and hindling incipiently developed. Postparaconal and premetaconal facets developed at the labial end of the lophs; short paraconal crest and low postparaconal, premetaconal and postmetaconal crests present on all molars; hypoloph of M_5 reduced. I_1 crown lanceolate, lacking enamel on lingual surface, long, nearly straight root; conspicuous, boss-like alveolar crest on dentary above the root of I_1.

Remarks. The cranium of *Hadronomus* appears to fit more comfortably with the Macropodidae than with the Potoroidae on the basis of its molar morphology, neurocranial sutural figuration and the presence of a well developed, cuspule-bearing lingual crest on the upper permanent premolar. The molars are basically similar to those of the Sthenurinae. However, as Woodburne (1967) implies, there are more synapomorphies between the Sthenurinae and the Macropodinae, particularly with the genus *Protemnodon*,

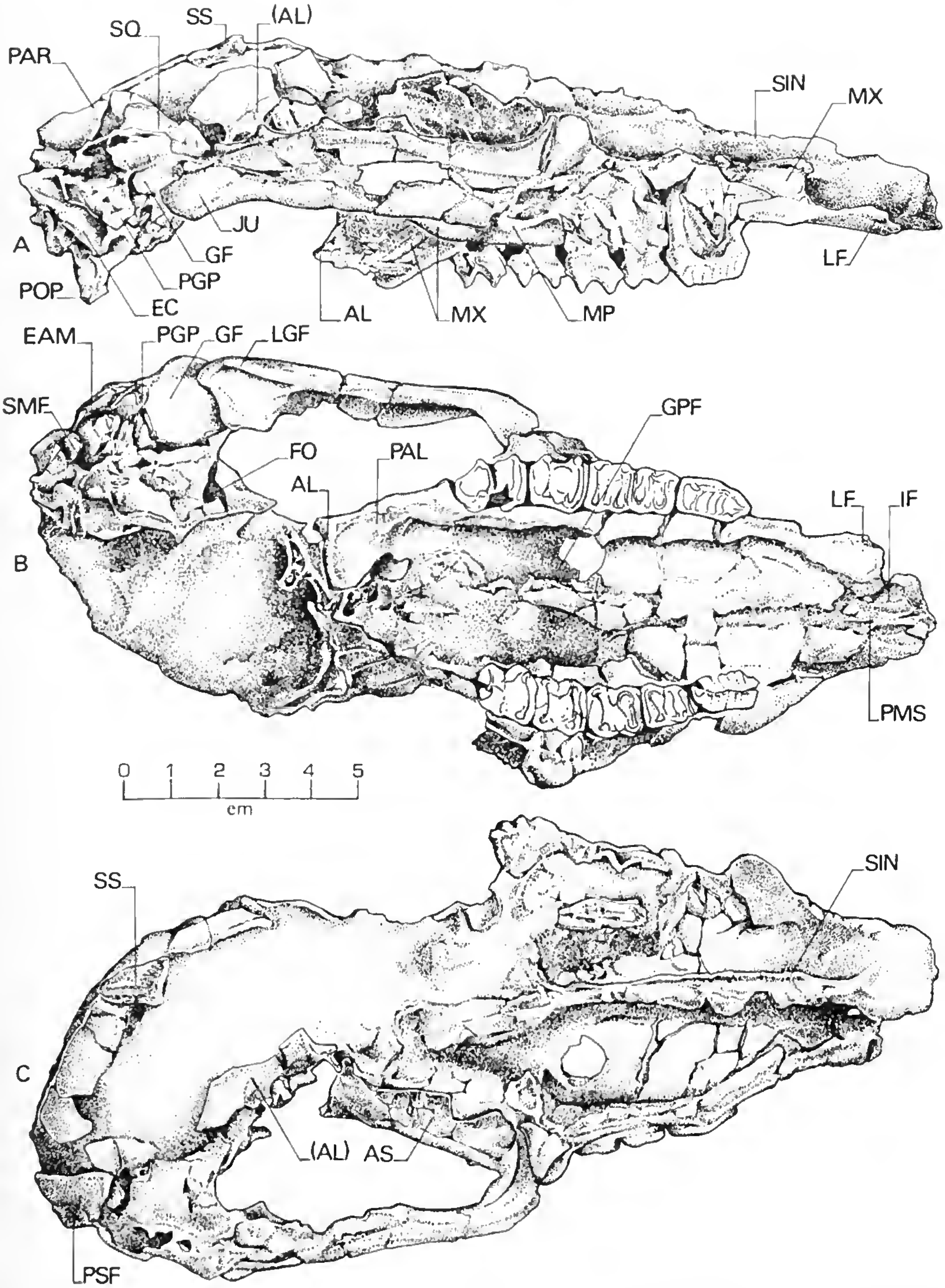

Fig. 1. Line illustration of *Hadronomus puckridgi* Woodburne, 1967: A, note straight, horizontal diastemal palate, long strap-like Jugal and posteriorly low neurocranium in lateral aspect; B, large palatine vacuities, straight profile of zygomatic arch and well-developed lateral glenoid process in lateral aspect; C, long squamosal sulcus, broad rostrum and braincase in dorsal aspect. Abbreviations: **PAR**, parietal; **SQ**, Squamosal; **SS**, sagittal suture; **AL**, position of alisphenoid; **SIN**, choanal septum; **MX**, maxilla; **LF**, lingual foramen or canine alveolus; **MP**, masseteric process;**AL**, alisphenoid; **JU**, jugal; **GF**, glenoid fossa; **PGP**, postglenoid process; **EC**, ectotympanic; **OP**, paroccipital process; **LGF**, lateral glenoid flange, **EAM**, external auditory meatus; **SMF**, stylomastoid fossa or sulcus; **FO**, foramen ovale; **PAL**, palatine; **GPF**, greater palatine fenestra; **IF**, incisive foramen; **PMS**, septal process of the premaxilla; **PSF**, postsquamosal foramen; **AS**, alveolar or suborbital shelf of the maxilla.

than there are between either of those subfamilies and *Hadronomus*. The plesiomorphic condition of the cranium of *Hadronomus* suggests that it is not directly related to either macropodid subfamily, both of which share many synapomorphic features in the zygomatic arch, orbit and neurocranium.

Description and Comparison

General description. The cranium of *Hadronomus* (Figs 1, 2) is significantly larger than any of the largest living macropodid species, being approximately the size of the crania of some *Protemnodon* species (Fig. 1). The neurocranium is low and broad with a triangular outline shape (Fig. 1B,C). The splanchnocranial region is horizontal with only a minimal expression of the sharp downward flexion of the antepremolar maxillary region typical of the majority of macropodines (Fig. 1A). The conspicuously elongated jugal has a flat, as opposed to a bowed contour, and maintains an almost constant depth from beneath the orbit to its flange-like termina-

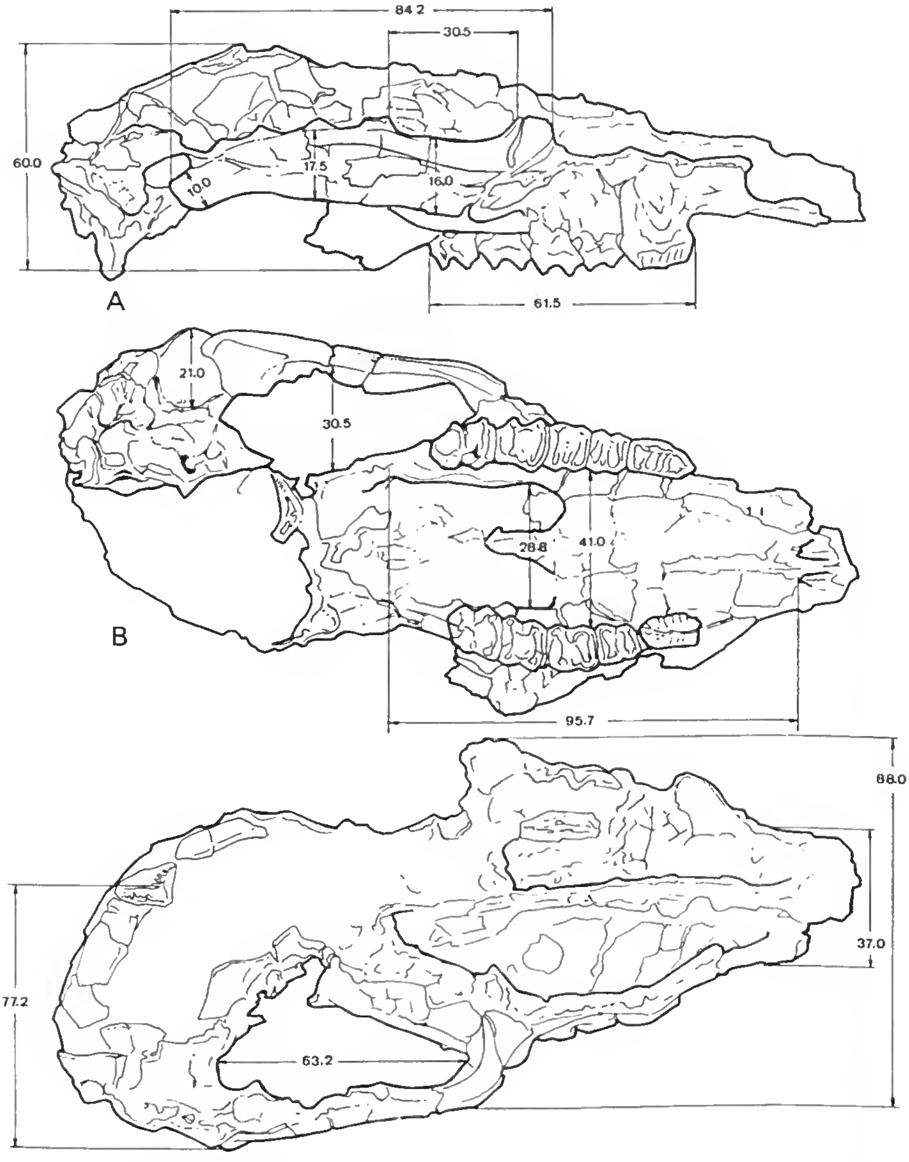

Fig. 2. Measurements (in millimetres) of the cranium of *Hadronomus puckridgi*: **A**, lateral aspect; **B**, ventral aspect; **C**, dorsal aspect.

tion lateral to the glenoid fossa. This contrasts strongly with the majority of living macropodine kangaroos among which the jugal tapers sharply away from the masseteric process. The masseteric process is a short, blunt anteroposteriorly directed crest of the maxilla in which the jugal does not participate. The glenoid fossa is wide, deep and confined laterally by a deep jugal crest and its internal lunette. The postglenoid process is comparatively stout. A remnant of the lambdoid crest indicates that the posterior portion of the neurocranium projected posteriorly over the occiput (Figs 3, 7A). The external auditory meatus is a low and broad aperture occupying most of the large, posteriorly inclined auditory arch.

The palate is broad, flat and relatively shallow to the alveolar margins. The posterior palate is invaded by large, partially divided greater palatine fenestrae. The cheek tooth rows are nearly straight, the curvature of the left cheek tooth row being exaggerated by post-depositional distortion (Fig. 1B). The incisive foramina are located close together on either side of the premaxillary suture. A labial foramen or small canine alveolus is present on the diastemal crest within the premaxillary-maxillary suture. The supradiastemal (buccinator) fossa is shallow. The contour of a remnant of maxilla on the left side (Fig. 1B,C) is similar to that of a Euro which implies that the rostrum was rather inflated immediately above the diastema.

The remnants of the neurocranium indicate that the back of the skull was low and broad. Although the frontal and alisphenoid are poorly preserved, a fragment of the parietal shows the most likely relationship of the sutures (Fig. 3). The alisphenoid takes an oblique anteroposterior course across the lateral wall of the braincase as in typical macropodines, indicating that the frontal did not make contact with the squamosal (Fig. 3). A small triangular fragment on the dorsal midline preserves the frontoparietal contact at the convergence of the frontal and sagittal crests. The trend of the frontoparietal (coronal) suture is acutely anterolateral as in mature *Macropus giganteus* and *Macropus rufa*.

Premaxilla. Although little of the premaxilla is represented, the approximate course of the premaxillary-maxillary suture can be traced from the posterior margins of the incisive foramina, anterolaterally to the diastemal crest. The suture appears to course posteriorly on the lateral surface of the snout immediately above the diastemal margin for about 15.0mm after which it ascends vertically for about 10.0mm then courses obliquely posteriorly. A small canine alveolus or a labial foramen is developed in the suture at the level of the posterior margins of the incisive foramina. The suture defines a short anteriorly directed process of the maxilla which terminates along the posterior margins of the incisive foramina. The incisive foramina are divided by a comparatively large, posteriorly invasive midline process of the premaxilla. The base of the premaxilla follows the same nearly horizontal trend as the maxillary diastema to the point where it is broken. It may be safely assumed that the rest of premaxillary palate also projected straight forward. The lateral profile of the anterior palatal region therefore more closely resembles that of the potoroids *Hypsiprymnodon* and *Potorous* than any of the typical macropodine kangaroos.

Maxilla. The maxillary palate is crushed, though largely intact. The original surface appears to have been shallowly concave posteriorly and flat in the diastemal area. As in potoroids and some primitive macropodines, large greater palatine fenestrae are present. These are long, parallel-sided ovoid vacuities, partially divided by a midline process and are similar in form and extent to those present in sthenurine kangaroos and the macropodine *Dorcopsis* (Figs 1B, 2B). The maxillary roots of both zygomatic arches are present, and by reference to both sides, the entire structure can be restored. In contrast to macropodines, the infraorbital fossa is indistinct and low. The surface of the maxilla immediately anterior to the orbit is convexly confluent with the jugal, rather than forming the long, oblique crest characteristic of macropodine kangaroos. The masseteric process of the maxilla is short, blunt and laterally compressed. Other than the masseteric process, it appears that the maxilla makes no further contribution to the zygomatic arch. Although the sutures are indistinct in this region it seems likely that the jugals extended a considerable distance (>10.0mm) anterior to the orbital margin. The morphology of the maxillary root of the zygomatic arch of *Hadronomus* thus differs from that of typical

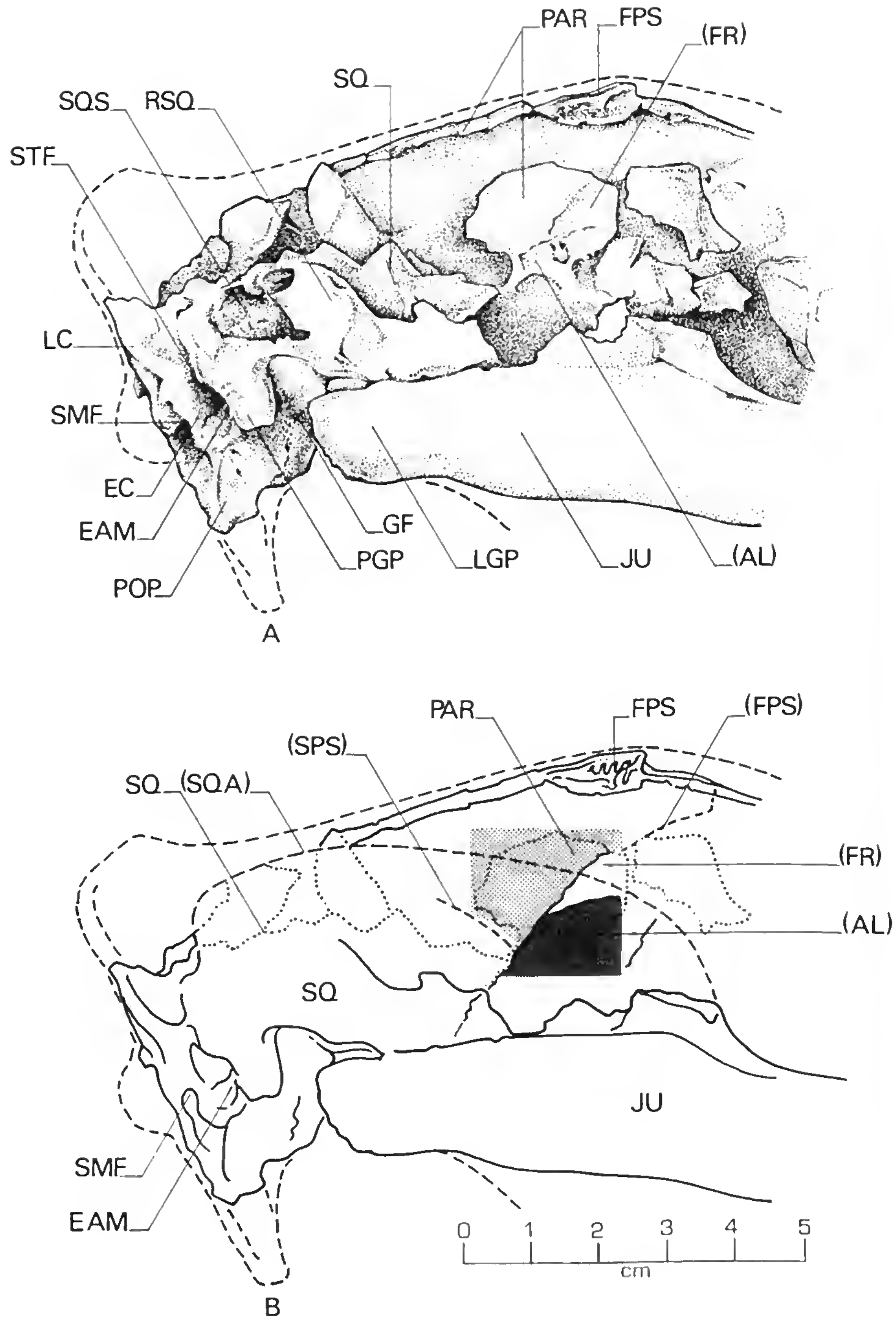

Fig. 3. Lateral aspect of the neurocranium of *Hadronomus puckridgi*; **A**, though badly damaged, the relations of the braincase laminae are preserved; **B**, schematic interpretation of the braincase wall. Additional abbreviations: **SQ**, remnant of squamosal; **SQS**, breached squamosal sinus; **STF**, supratympanic fossa; **LC**, lambdoidal crest; **FPS**, frontoparietal suture; **FPS**, projection of the frontoparietal suture; **FR**, posterior-most position possible of the frontal bone; **SQA**, postulated outline of the missing squamosal portion of the zygomatic arch.

macropodines in having a short, poorly developed anteorbital crest, an indistinct, low infraorbital sulcus and a broad preorbital process of the jugal, in essence a condition intermediate to potoroines and macropodines.

The suborbital shelf of the maxilla is a platform-like structure; wide laterally but shallow dorsoventrally and distinctly tapered posteriorly. It is about half as deep as the equivalent structure in *Macropus rufa* and *Macropus robusta*. The alisphenoid and palatine sutures are poorly defined in the postalveolar region of the shelf, but a long, low, mesially extensive postalveolar process of the maxilla is present (Fig. 1A,B). The infraorbital canal lies at the anterior extremity of a deep oval fossa, the lateral margin of which developes into a distinct, rounded crest forming the dorsal contour of the entire length of the suborbital shelf. The suborbital region of *Hadronomus* is thus quite distinct from that of the larger macropodine kangaroos and resembles somewhat the potoroine condition, in which the shelf strongly tapers off posteriorly. It is however, proportionally deeper than that of *Potorous tridactyus*, more resembling the condition in *Aepyprymnus*. The suborbital sutural morphology is obliterated by numerous cracks and cannot be traced.

Zygomatic arch. A striking feature of *Hadronomus* is its long, straight, strap-like jugal. It differs from that of macropodine kangaroos in maintaining an almost equal width for about two-thirds of its total length (Figs 1, 7). This condition is accentuated by the virtual absence of an anterior jugal eminence and the development posteriorly of a deep lateral glenoid crest with a blunt margin. The dorsal margin of the jugal describes the inferior border of the orbit emarginated behind by a prominent postorbital process; posterior to which the squamosal-jugal contact continues on in a smooth, gently arcing suture. The orbital notch is comparatively shallow giving the impression that the orbit was somewhat more elliptical than the typically round macropodine condition. The masseteric crest is correspondingly long and faithfully follows the dorsal profile for about three-quarters of the length of the bone. In most, if not all macropodine kangaroos, the masseteric line is composed of two distinct arcs or describes a wide V-shape.

A straight, nearly horizontal inscription can be seen on the jugals of *Aepyprymnus*, although its inferior jugal border strongly tapers toward the glenoid fossa, commencing in line with the base of the postorbital process. The inferior margin of the jugal of *Hadronomus* is relatively much thicker and more rounded in contrast to the thin, tapered margins of the large living macropodines. The jugal of the sthenurine kangaroo, *Sthenurus atlas*, bears a resemblance to that of *Hadronomus* in having a comparatively straight masseteric line.

The lateral glenoid crest or eminence encloses a 5.0mm deep lunate depression that forms the anterolateral portion of the glenoid fossa. Its posteroinferior margin is roughened, presumably for the lateral craniomandibular ligament. The lateral glenoid eminence is present in the larger macropodine and sthenurine kangaroos, but in *Macropus* sp. it is not remotely developed to the extent found in *Hadronomus*. The lateral glenoid eminence is strongly expressed in *Sthenurus* (*Simosthenurus*) species. From the lateral aspect, the deep, rounded posterior margin of the jugal in *Sthenurus maddocki* appears very similar to that of *Hadronomus*. However, in ventral aspect the fossa is relatively smaller and shallower due to the thick, ventromedially tapering base of the crest. Palorchestines (*Propalorchestes*, *Palorchestes*) are the only other diprotodontans having an equivalent degree of development of this structure. Living potoroids typically lack a lateral glenoid eminence.

The anterior orbital surface of the jugal bears a deep, oval preocular or "lacrimal" fossa situated superolateral to the infraorbital canal opening. In the majority of macropodines this structure is fairly shallow and is often more of a deep, crescentic groove. Although variable in both subfamilies, it tends to be a very deep, ovoid structure in potoroids and therefore similar to that of *Hadronomus*. The position of this fossa within the orbit is also significant in that it is situated in the inferolateral margin of the orbit in macropodines, some distance behind the anteriormost extent of the orbital margin. In potoroids it opens at the anterior extreme of the orbital fossa. With respect to its position, *Hadronomus* is more like the potoroids due to the more anterior extent of the jugal.

The squamosal portion of the zygomatic arch is poorly preserved. The broken edges of the process indicate that it was moderately

deep and relatively long. The squamosal sulcus is very long and less slanted anteroposteriorly than in *Macropus* spp.

The glenoid fossa is wide and flat. The transverse axis of the articular surface is greater relative to its length, although its basic shape does not differ significantly from that of the larger *Macropus* species. The increased transverse width of the fossa is reflected in the marked lateral deviation of the marginal profile of the squamosal adjacent to the fossa. The postglenoid process is large and projects ventrolaterally as opposed to the more or less ventral projection of the structure in living *Macropus*. The combined structures of the lateral glenoid eminence and the large ventrolaterally projecting postglenoid process result in a deep, posterolaterally confined fossa, although its large dimensions and the flat articular surface indicate that the condyle was very mobile, as in other kangaroos. The overall construction of the glenoid region is very similar to that of the Sthenurinae, implying that the dentary condyle of *Hadronomus* was likewise transversely elongated and large.

Neurocranium. The dorsal surface of the neurocranium is not preserved. A portion of the lateral wall of the braincase is present, sufficient to determine the basic sutural configuration (Fig. 3). The thin, overlapping sutural margin of the squamosal lamina is entirely missing and separated from the parietal fragment by a gap about 7.0mm wide. It is likely that the squamosoparietal suture was located near the posterior edge of the parietal fragment, and may have overlapped it a short distance. However, there are no sutural crenulations present on either surface. The anteroinferior surface of the parietal fragment is inscribed with a fine crest which I interpret to be the posterior margin of the alisphenoid and therefore the actual trend of the alisphenoidoparietal suture. The height and angle of this sutural line indicates that the anterior process of the parietal was long and that the course of the frontal towards the squamosal was interrupted by the alisphenoid. A second, almost vertical crest that intersects the alisphenoid crest may represent a faint infratemporal crest or the posterior-most extent of the frontal, which in any case is overlapped by the alisphenoid and does not necessarily indicate that the separation of the squamosal from the frontal was narrow. Given the angle of the frontoparietal suture projected from the bone fragment conveniently retaining the sagittal-frontal crest confluence, the frontoparietal suture was at an acute angle and coursed a considerable distance anterior to the anterior edge of the squamosal. It can be concluded therefore that the sutural arrangement was like that of the macropodine kangaroos rather than the potoroids. This character is no longer considered to be a consisent feature for differentiating macropodids from potoroids because a recently discovered fossil *Hypsiprymnodon* species has the frontal separated from the squamosal by the alisphenoid (Flannery and Archer 1987a) and this is also the case in *Bettongia moyesi* (Flannery and Archer 1987b). Other examples of this inconsistancy within specific clades are known, for example in the thylacoleonids (Murray *et al.* 1987). In the case of *H. bartholomaii* Flannery and Archer, 1987a, the condition may be an allometric effect because there is a considerable size difference between the two species. In this regard, it would be interesting to examine that region of the cranium of the Pleistocene giant musk-rat kangaroo, *Propleopus oscillans*.

In both macropodoid groups, the course of the frontoparetal suture is extremely variable and changes ontogenetically in conjunction with the gradual convergence of the frontal and temporal crests. Although the sutural figuration is not an entirely stalwart attribute, being ontogenetically and phyletically inconstant, the general trend is no less real. The top of the braincase, the entire frontal and nasal roof is missing. The small triangle of convergent parietals denotes the vertex of the cranium, and although the specimen is squashed, the integrity of its outline is preserved, leaving little doubt that the braincase was low and fairly broad. In macropodine kangaroos, the greatest breadth of the cranium is across the zygomatic arches, a considerable distance anterior to the glenoid fossa. In *Hadronomus* the greatest breadth of the cranium is significantly further back, at the level of the glenoid fossae. This imparts a triangular profile to the restored cranial outline (Figs 2C, 7B) and in this respect the cranial outline and its flat zygomatic arches is not unlike phalangerids and the primitive diprotodontoid *Ngapakaldia*.

Cranial base. The basicranial axis is represented by a nondescript fragment of pre-

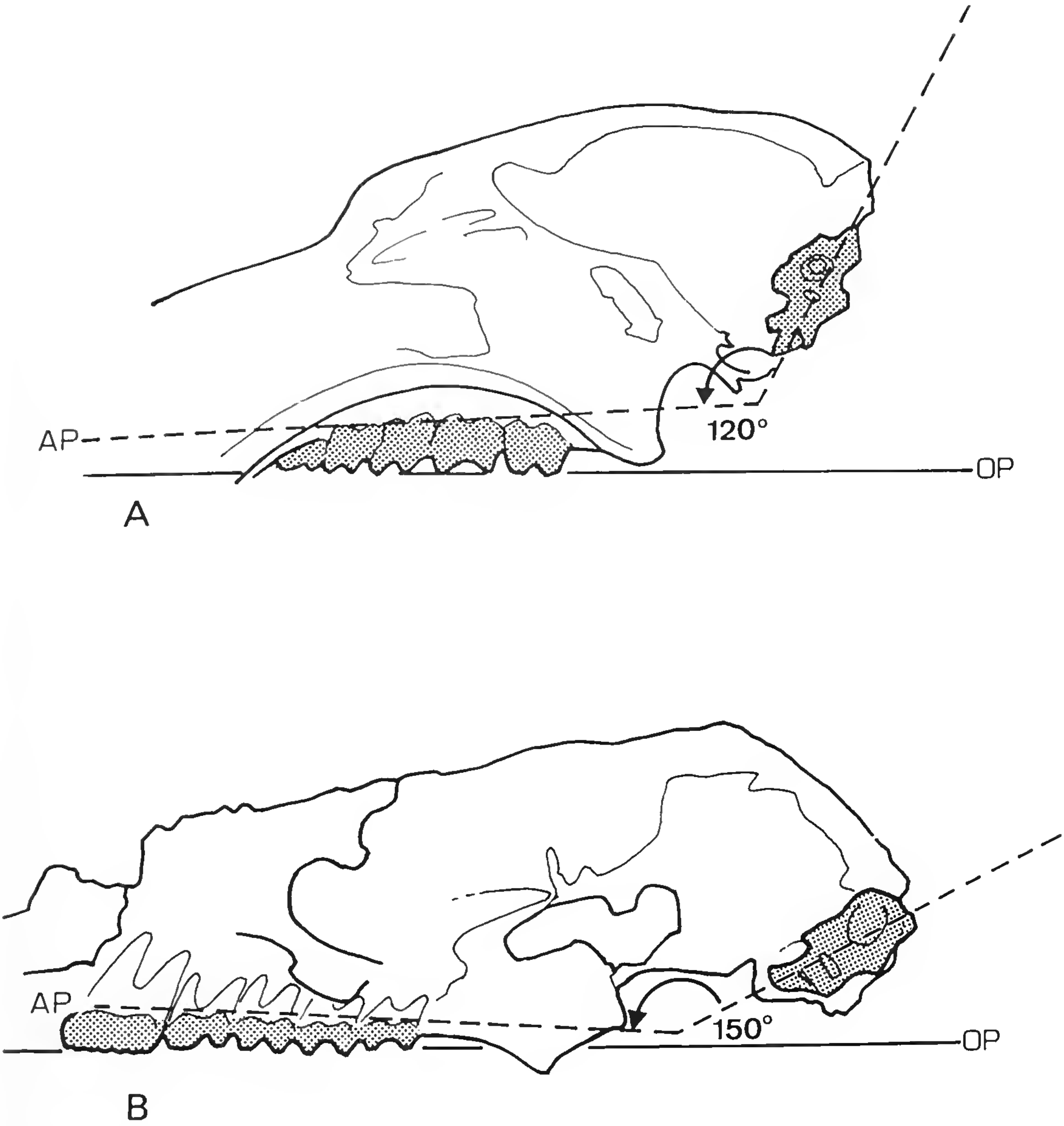

Fig. 4. Comparison of the position and orientation of the petrosal in **A**, *Macropus robustus* and **B**, *Hadronomus puckridgi*, giving an indication of the difference in basicranial flexion between the two genera. Abbreviations: **OP**, occlusal plane; **AP**, alveolar plane, defined by the cemento-enamel junction. Note that A, *Macropus* is drawn from a sagittal section which illustrates the lingual side of the dentition whereas the buccal side of the cheektooth row is figured in **B**, *Hadronomus*.

sphenoid. The base of the neurocranial wing of the alisphenoid is present immediately anterior to the squamosal zygomatic process. The position of the anterior end of the pterygoid fossa is indicated by a bifurcation of the posteroinferior margin of the pterygopalatine process. A small portion of the alisphenoid is attached to the low, mesially wide maxillary postalveolar process. Both the palatine and pterygoid processes are missing (Figs 1A,B, 7A). The basicranial axis and palatal plane is considerably less deflected than in *Macropus* (Fig. 4A,B). In the absence of the occipital condyles, the low angle of the cranial base in *Hadronomus* is indicated by the position of its petrous bone which lies scarcely above the occlusal line.

Orbit. The sutural contacts within the orbit are lost in a maze of cracks. The basic shape of the orbital fossa is slightly elliptical

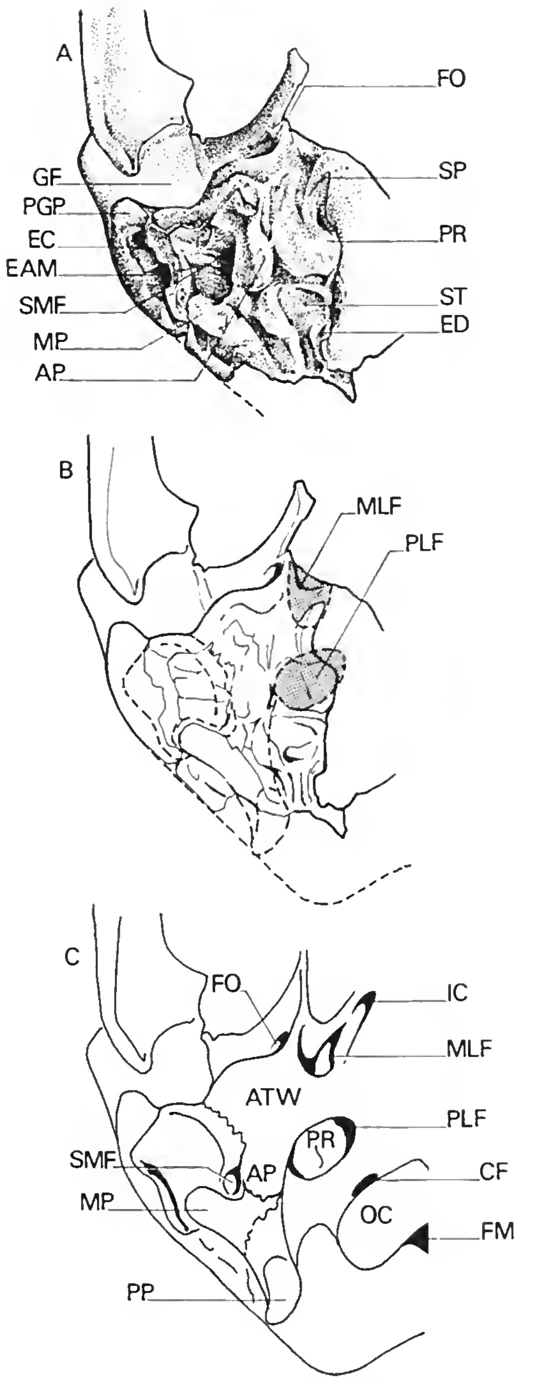

Fig. 5. Interpretation of the relations of the auditory region of the neurocranium of *Hadronomus*: A, poorly preserved surface anatomy of right side of the basicranium; B, approximate positions of the major landmarks sketched in; C, schematic interpretation of the structures. Abbreviations not previously defined: **IC**, internal carotid foramen; **SP**, superior process of the petrosal; **PR**, body of the petrosal; **ST**, sulcus representing the sigmoid portion of the transverse sinus; **AP**, alisphenoid portion of the paroccipital process; **MP**, mastoid portion of the paroccipital process; **ED**, endolymphatic duct; **MLF**, median lacerate foramen; **PLF**, posterior lacerate foramen; **PP**, paroccipital process; **OC**, occipital condyle; **CF**, condylar foramen; **ATW**, alisphenoid tympanic wing; **FM**, foramen magnum.

and perhaps relatively more elongated, smaller and deeper than in *Macropus* spp. The orbital margin of the jugal differs from macropodine kangaroos in being slanted mesially as opposed to being everted laterally. The lateral portion of the margin is thin and sharp in contrast to the wide, flattened emargination present in macropodines and sthenurines. Thin, sharp orbital margins are present in potoroid kangaroos. However, the orbital margin of *Hadronomus* appears to be trending towards the condition in *Macropus* with respect to its conspicuous mesial slant. If this trend were carried further, i.e. the jugal margin folding in on itself, a broad orbital emargination of the sort found in *Macropus* spp. would be the result. The lack of elaborate suborbital sculpturing in the jugal of *Hadronomus* accounts for the apparent lack of marginal eversion.

Auditory region. The superficial structures of the auditory region are scarcely represented and the remaining structures are badly damaged by large, wedge-shaped cracks. However, there is a sufficient representation of the middle ear region to elicit broad comparison with other macropodoids. In lateral aspect (Fig. 1A) the most obvious feature is the elongated, posteriorly slanted auditory arch occupied by a large, elliptical remnant of the ectotympanic. The ectotympanic is severely damaged, but it appears to have been anteroposteriorly attenuated and relatively large in diameter. The entire postsquamosal region, including a small remnant of the lambdoidal crest is slanted posteriorly in contrast to the nearly vertical relations of these structures about the external ear in *Macropus giganteus*, *M. rufa* and *M. robustus*. The ventral portion of the ectotympanic is comparatively thick and cancellous internally as in the sthenurine kangaroos. A ventral crest could have been present. Dorsally, the bone of the ectotympanic becomes very thin and may have been incomplete in its posterodorsal extremity. The opening of the ectotympanic tube (external auditory meatus) is less posteriorly directed and probably significantly shorter than in the large *Macropus* species (Fig. 5).

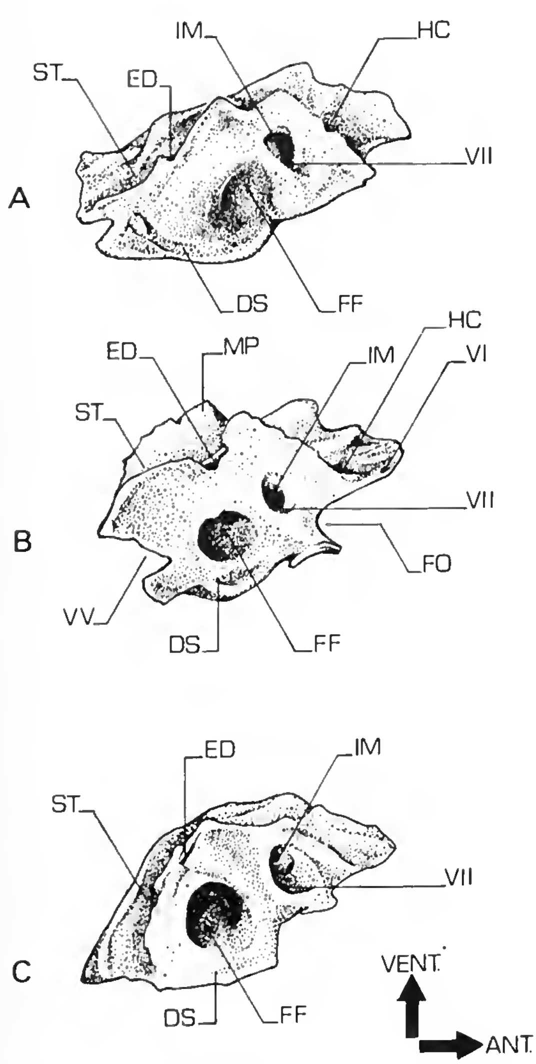

Fig. 6. Comparative morphology of the petrosal bones of **A**, *Hadronomus puckridgi*; **B**, *Macropus robustus*; **C**, *Potorous tridactylus*. Note the large, ovoid shallow floccular fossa **FF** in *Hadronomus*. Abbreviations: **HC**, canal hiatus of the facial nerve; **IM**, internal acoustic meatus; **ED**, endolymphatic duct; **ST**, sulcus for the sigmoid portion of the transverse sinus; **VII**, facial nerve canal; **VV**, posterodorsal notch of petrosal surrounding the anastomosis of the postglenoid and postzygomatic venous channels, the posterior extremity of which is damaged in *Hadronomus*.

The alisphenoid tympanic wing appears to have been broader and more inflated than in *Macropus* spp. Other macropodines, for example the Nail-tailed Wallaby, *Onychogalea unguifera*, have proportionally broad, inflated alisphenoid tympanic wings. Remnants of the mastoid and paroccipital processes are present on the specimen. Neither of these structures appear to differ in any particular way from the basic macropodoid morphology in which the alisphenoid and mastoid contribute flying buttress-like processes to the base of the paroccipital process. Judging from the thickness and steep angle of the break in the alisphenoid tympanic wing at the base of the paroccipital process, it is reasonable to assume that it contributed a substantial descending process, as in macropodids. The extensive broken basal portions of the process indicates that it was a robust structure, as large as that of *Macropus rufa*.

Immediately inferior to the ectotympanic, near the base of the paroccipital process there is a deep, vertically elliptical fossa which I have labelled as the stylomastoid fossa in Figs 1 and 3. It does not have the appearance of a breached paroccipital sinus, and appears to have a sulcus running anteroinferiorly from the opening, presumably for the facial nerve. In Fig. 5C, I have attempted to restore the overall relationships of the damaged superficial structures of the auditory region.

The ventral and internal surfaces of the well-preserved petrosal are exposed. The orientation of the petrosal of *Hadronomus* differs from that of *Macropus robustus* in being less inclined towards the vertical by about 30 degrees relative to the approximate horizontal plane of the toothrow (Fig. 4). The outline shape of the petrosal of *Hadronomus* is more elongated and narrower than in *Macropus robustus*, resembling more closely that of *Potorous tridactylus* (Fig. 6). The mastoid process of the periotic is much smaller and more horizontally oriented and the "jugular" process appears to be less prominent. As in potorids, the sulcus for the sigmoid portion of the transverse sinus is a distinct, broad channel with a fossa-like widening about midway along its course. In *Macropus robustus* it is a simple, trough-like groove. The ventral crest on the superior periotic process appears to have been thin and the medial surface of the process at the hiatus of the facial canal is smooth as opposed to rugose.

Although there are several more contrasts of a minor nature, I will mention only one more difference in the petrosal morphology which may be of some importance. In as many specimens of kangaroo petrosals as I have been able to examine, the floccular fossa

is very deep and undercut internally, behind its sharply defined orificial crest. *Hadronomus* has a large, oval, exceptionally shallow, floccular fossa with very rounded orificial margins (Fig. 6A). Although not as large in proportion to the body of the petrosal, the floccular fossa of *Hadronomus* resembles that of the hairy-nosed wombat, *Lasiorhinus latifrons* as much as it does any of the living kangaroo specimens used in this description.

The presence of a shallow floccular fossa (a "vombatiform" character) in *Wynyardia bassiana* was a primary argument by Archer (Archer 1984; Aplin and Archer 1987) against its having phalangeridan affinities, as postulated by Haight and Murray (1981). However, its value as a functionally related character has been overshadowed by its apparent systematic importance. The shallow floccular fossa is a direct reflection of the size and shape of the paraflocculus of the cerebellum. The flocculi are intimately related to the vestibular nuclei and their relative degree of development is closely associated with the extent to which balance and spatial orientation are important to the animal's locomotor repertoire (Sarnat and Netsky 1981). The flocculi are therefore greatly expanded laterally in agile arboreal species, such as primates and phalangeroid marsupials, fleet bipedal cursors (kangaroos) and in lower vertebrate forms with well-developed lateral line systems. The flocculi are relatively reduced among slow-moving quadrupedal mammals and in general, among all terrestrial vertebrates (Sarnat and Netsky 1981).

The comparatively poorly developed flocculus of *Hadronomus* may be an indication that these were slow-moving kangaroos with a high degree of stability in their stance and gait. As speed and maneuverability are usually sacrificed for stability, it is likely that these were not specifically adapted to wide expanses of open habitat, as its name, "large wanderer" seems to imply. I have not been able to examine the floccular fossae of the petrosal of a sthenurine, but Tim Flannery (personal communication) informed me that they are also shallow.

Dentition. The crown morphology of *Hadronomus* is described in detail by Woodburne (1967). A few observations on the gross morphology of the cheek tooth row can be added to his assessment. Although the crowns of the upper molars lengthen progressively from front to back, the total crown height (cementoenamel-junction to loph apex) decreases slightly from front to back. In macropodines, including protemnodonts, the crowns increase in height from front to back. Crown heights decrease from anterior to posterior in rat kangaroos (*Potorous*, *Hypsiprymnodon*, *Bettongia*) and, particularly M_{3-5}, in some sthenurines (see Tedford 1966, Fig. 3). The slanted implantation angles of the cheek teeth of *Hadronomus* are indicative of a high degree of mesial drift, an uncommon feature in potoroids, but characteristic of macropodine kangaroos. A feature present in the molar dentition of ASP889, to which I attach some significance further on, was not figured or described by Woodburne (1967). This is the formation of a cleft between the postparaconal crest and the formation of a cleft between the postparaconal crest and the buccal cingulum that resides on the labial margin of the interloph valley. The structure diminishes serially from M_2 to M_4 and is absent in M_5. In *Hadronomus* it is the site of the postparaconal wear facet described by Woodburne (1967).

DISCUSSION

The foregoing morphological description of *Hadronomus*, in which many of its features seem to be more comparable to those of potoroids than macropodids, might give the erroneous impression that the cranium of *Hadronomus puckridgi* resembles that of a potoroid. In fact, its overall appearance is that of a generalized macropodid, a bit protemnodont-like in lateral profile and somewhat sthenurine-like in specific features (Fig. 7). This is because the combined features normally used to phenetically discriminate macropodid from potoroid crania are really quite subtle and formally depend primarily on the character of the dentition and the possession in the latter, of a long, narrow, horizontal premaxilla.

As Woodburne (1967) observed, the cheek tooth morphology of *Hadronomus* is basically similar to that of the protemnodont macropodines and more specifically similar to that of the sthenurine kangaroos, especially in its possession of sharp, thin, evenly curved lophs and wide open, round-basined mid-valleys with incipient mid-links. Sthenurine-like too, are the level, wide, though short and

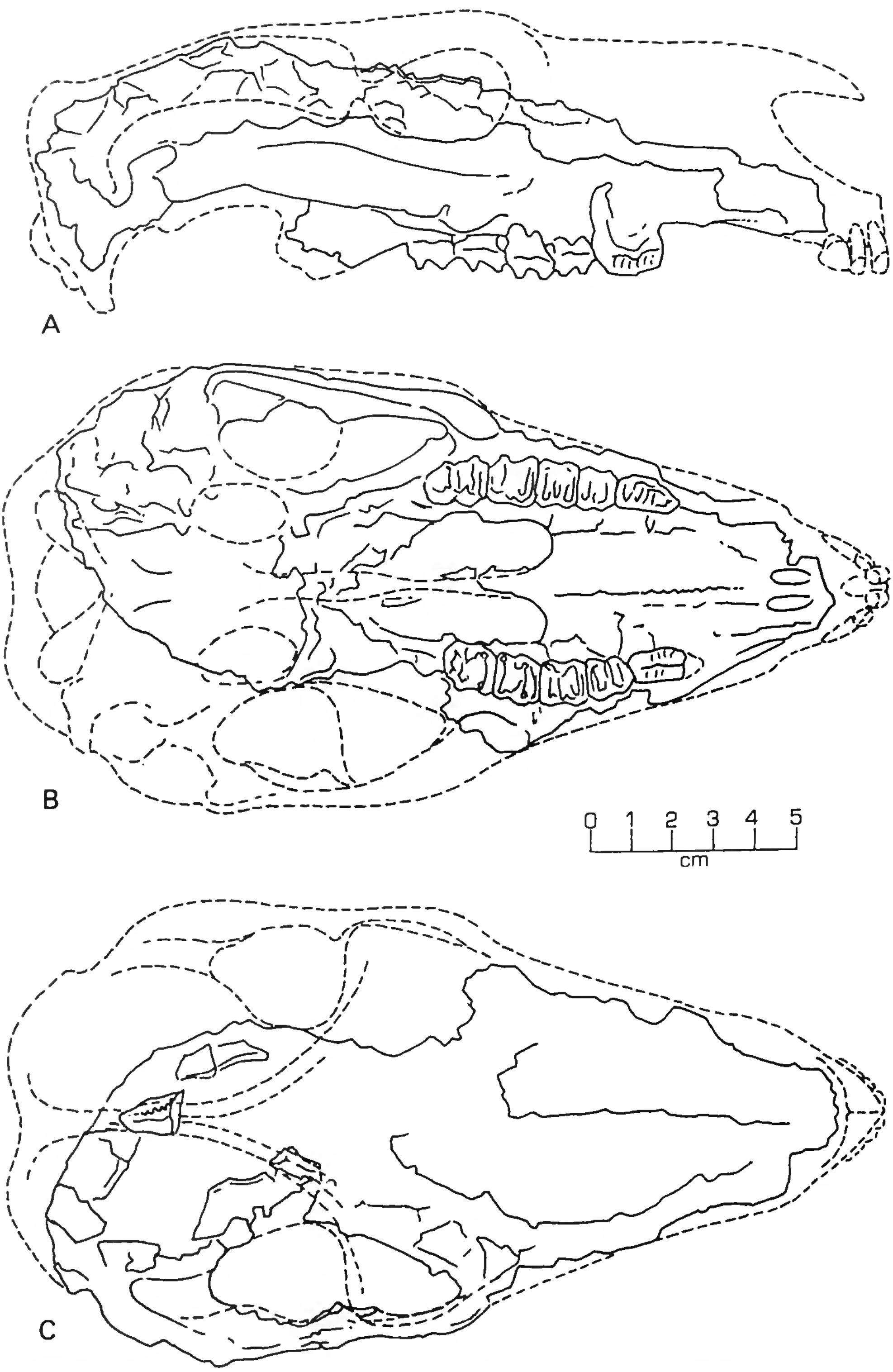

Fig. 7. Restoration of the cranium of *Hadronomus puckridgi* resulting in a lateral cranial profile reminiscent of *Protemnodon*: **A**, lateral aspect, note jugal morphology, low neurocranium; **B**, ventral aspect; showing invasive palatine vacuities and posteriorly broad cranial outline, relationship of the posterior portion of the jugal corrected to match lateral margin of the glenoid fossa. Profile of the nasals, alveolar portion of the premaxilla and the anterior frontal region is unknown; reconstruction is based on a minimal expression of features; **C**, dorsal aspect.

deep, shelf-like precingulae and enamel swellings along the buccal cusp bases.

The presence of a distinct labial link and distinct pre- and post-paraconal and metaconal crests are also suggestive of sthenurine molars. However, Sthenurines lack the conspicuous labial sulcus dividing the buccal crests in the interloph valley and the associated postparaconal and premetaconal facets apparently created by the rocking of the hypoconid at the end of each masticatory stroke.

The retention of prominent individual cusp points is a more subtle feature of *Hadronomus*'s molars. The individual cusps seem to become increasingly prominent as the lophs are reduced by wear. This trait is present to a far less extent in Sthenurines and not at all evident in *Protemnodon*. An analogous condition is present in the bilophodont molars of the folivorous colobine monkeys (Cercopithecidae) in which initial punctures by the prominent cusp points help to retain tension on the thin flexible leaf surface during the shearing process. They also initiate tearing of tough, thin vegetable matter by point-shearing (Walker and Murray 1968). *Hadronomus* is therefore a specialist folivore of some kind, my guess is that predominately they ate rather large, thin leaves as opposed small, thick, tough leaves such as *Acacia* phyllodes, which would require a component of crushing and less excursive, though more powerful shearing. This may be the basic difference functionally between the sthenurine dentition and that of *Hadronomus*.

The postparaconal and premetaconal facets seem to indicate that *Hadronomus* had a considerable axial rotation of its dentary during lateral excursion. This may explain the large lateral glenoid process which would have to accommodate a large rotational moment simultaneous with each side to side component of mastication.

The dentary, also previously described by Woodburne (1967) is practically unique among macropodoids for its exaggerated posterior depth, which however, is no greater than that seen in *Sthenurus brownei*. The dentary differs from the Sthenurinae principally in having a long, nearly horizontal symphysis, its relative thinness and in its flat medial and lateral surfaces. The diastemal crest abruptly terminates high above the alveolar sulcus of I_1 rather than tapering gradually towards the incisor root. It also lacks the posterior mental foramen, a consistent synapomorphic feature of the Sthenurinae (Tedford 1966).

The dentition of *Hadronomus* is therefore similar enough to that of the sthenurines to allow for a possible ancestral relationship, although lacking any derived sthenurine features and being somewhat specialized functionally. Its molars appear to be less like those of protemnodont macropodines, although it is also possible to derive them from *Hadronomus*, as Woodburne (1967) observes.

Because the Sthenurinae appear to share a number of cranial synapomorphies with the macropodinae, including elevation of the cranial base high above the tooth row and detailed similarities in the zygomatic arch, orbit and prezygomatic portion of the maxilla (Tedford 1966) a direct ancestral relationship with the sthenurines seems unlikely. A direct cladistic connection with the protemnodont macropodines is however more remote due to the greater similarity of the dentition of *Hadronomus* to that of *Sthenurus*.

The plesiomorphic cranium of *Hadronomus* has relatively few unambiguously synapomorphic features in common with the Sthenurinae. In sthenurines, the jugal and maxilla are jointly produced forming a strong downward directed masseteric process. In *Hadronomus* the jugal is not involved. Like sthenurines, *Hadronomus* has large palatine vacuities and narrow palatine bars. It also has a thick, cancellous ectotympanic, as in the sthenurinae, but it is not known for sure whether it was long or ventrally keeled. Unlike sthenurines, the diastemal palatal surface does not appear to have been exceptionally short.

The most convincing similarities between *Hadronomus* and sthenurine crania are in the glenoid fossa morphology. The deep posterior jugal eminence, laterally expanded glenoid articular surface and the more lateral position and orientation of the postglenoid process form a possible constellation of synapomorphic features.

Hadronomus has a greater subjective resemblance with *Protemnodon* in cranial shape, which is elongated, low and broad posteriorly (Bartholomai 1973). However, the zygomatic arch morphology, degree of rostral decurvation, lack of palatal vacuities, deep suborbital shelf, long, delicate masseteric processes and the basically macropo-

dine features of the maxillary root, i.e. the sharply defined, long and oblique prezygomatic sulcus are all good macropodine synapomorphies that are conspicuously absent in *Hadronomus*. Consequently, I am reluctant to place *Hadronomus* in either subfamily as its cranial morphology seems to bear no closer relationship to one or the other. Moreover, the protemnodont macropodines and the sthenurines appear to be more closely related to one another with respect to cranial morphology than *Hadronomus* is to either. Indeed it has been suggested by Tedford (1966) that the sthenurines were derived from the macropodines. These similarities might be due to parallelism, but this possibility seems to be weakened by the radically different adaptive zones expressed in their respective morphologies.

This implies that another clade may be involved. With regard to systematics, *Hadronomus* can remain as macropodid Subfamily *Incertae Sedis*, assigned to one or another of the existing subfamilies (?Balbarinae, ?Macropodinae), placing considerable strain on their diagnoses, or its rank could be elevated to Subfamily status. Alternatively, the few ambiguous *Hadronomus-Sthenurus* synapomorphies, such as the glenoid fossa characters, could support an argument for its inclusion in the Sthenurinae, provided that the macropodine synapomorphies of sthenurines and macropodines are redefined as parallelisms or symplesiomorphic features as per Flannery (1983). However, *Hadronomus puckridgi* itself is geologically too late to be ancestral to these subfamilies. Both sthenurine and macropodine kangaroos appear to be present at Alcoota (Woodburne 1967).

The plesiomorphic cranium of *Hadronomus* emphasizes the uneasiness of the division between potoroid and macropodid kangaroos. The differences between the cranium of *Hadronomus* and certain potoroids are primarily a matter of degree. The cranial base of *Hadronomus* is not as low as in *Potorous tridactylus* or *Aepyprymnus rufescens* nor is it as elevated as the majority of macropodine and sthenurine kangaroos. The suborbital shelf, pterygoid fossae and basicranial relations of *Hadronomus* are proportionally similar to those of *Aepyprymnus* but embued with macropodid refinements such as the presence of an at least incipient auditory tube on the ectotympanic. On the other hand, the morphology of the petrosal appears to be very conservative.

Summary of Cranial Characters in *Hadronomus puckridgi*

Cranial base and Palate

1. Straight diastema and diastemal palate
2. Large confluent palatal vacuities
3. Straight basicranial axis, posterior neurocranium low
4. Shallow, posteriorly tapering suborbital shelf

Neurocranium

5. Parietal-alisphenoid sutural figuration
6. Acutely convergent parietofrontal sutures
7. Lambdoid crest overhangs occiput, low broad braincase

Zygomatic arches

8. Jugal straight, flat; anteorbital process long, broad
9. Jugal parallel-edged, not wedge-shaped
10. Low, shallow prezygomatic sulcus
11. Short, blunt crest-like masseteric process
12. Prominent lateral glenoid eminence and postglenoid process
13. small, elliptical orbital fossa with thin orbital margins
14. Long, nearly horizontal squamosal sulcus
15. Cranium widest across glenoid fossae
16. Lacrimal fossae large, extend anterior to orbit

Auditory region

17. Petrosal low, oriented at a very obtuse angle
18. Floccular fossa of petrosal large, shallow, oval
19. Mastoid petrosal process small, nearly horizontal
20. Auditory arch low, broad, posteriorly slanted
21. Large, broad, thick, cancellous ectotympanic
22. Alisphenoid tympanic wing broad, slightly inflated

Dentition

23. Long sectorial permanent premolar; lingual crest
24. Straight cheektooth row, low near equal-height crowns
25. Bilophodont, weak links, wide cingulae

26. Thin, trenchant curved lophs, thin enamel
27 Double crest in buccal interloph valley
28. Lack of enamel on lingual surface of I_1

Dentary

29. Posteriorly deep horizontal ramus
30. Steep alveolar boss above lower incisor root

Woodburne's (1967) systematic conclusions with regard to the derived sthenurines drawn from the tooth crown morphology of *Hadronomus* remain little modified by the additional information of the skull. *Hadronomus puckridgi* represents a primitive macropodid with certain characters that "anticipate" the derivation of the protemnodont macropodines and sthenurines. The cranium appears far less committed to either group than the macropodines and sthenurines are to each other. However, the possible synapomorphies between sthenurines and macropodines (large masseteric process, wide protolophid on M_1, lingual cingulum on P_3, reduced parastyle on M_1, loss of canine etc.) can all be attributed to parallel responses to a dietary shift from omnivory to browsing (Flannery 1983). It is therefore questionable as to whether the sthenurines are any closer to the macropodines than *Hadronomus*. One potentially useful feature of *Hadronomus* is the lack of an enamel coating on the lingual side of the crown of I_1, (Woodburne 1967) presumably a plesiomorphic condition, which clearly distinguishes it from the derived Sthenurinae. In sthenurines (except for *Lagostropheus*) the enamel is wrapped around the lingual surface (Flannery 1983).

Flannery (1983) regards *Lagostropheus* to be structurally the most primitive member of the Subfamily Sthenurinae based on a substantial inventory of synapomorphies. *Hadronomus* possesses no derived characters in common with *Lagostropheus*, that might be anticipated if the genus were directly ancestral to the Sthenurinae. Thus, as Flannery (1983) points out, while there are no specific features of *Hadronomus* that would rule out a relationship to the sthenurines, there are no convincing synapomorphic features to support its inclusion within the subfamily.

There can be little doubt that *Hadronomus* is a plesiomorphic representative of the basic macropodid clade from which the macropodines and sthenurines probably originated, but they appear to be too primitive cranially, too specialized dentally and too late geologically to be directly ancestral to either subfamily. Based upon current information, they appear to be the end of the line for a group of primitive macropodids that gave rise to no subsequent lineages.

The only other kangaroos presently known that may show a relationship to *Hadronomus* are the mid-Miocene Balbarinae and the Subfamily Indeterminate *Galanarla tessellata* (Flannery *et al.* 1982). Although much smaller, possessing dentaries of a much different shape and more primitive dentally, balbarines express a number of features in their lower dentitions that are vaguely suggestive of a possible shared ancestry with the late Miocene Alcoota genus.

There is a broad similarity in the simple low-crowned bilophodonty, proportions and shape of the lophs and relative (weak) development of the fore and midlinks, and bulbous crown-bases possessed by the two genera. However, balbarines have a distinctive M_2 morphology in which the trigonid is low and markedly narrow, the compression being due to the lingual offset of the protoconid (Flannery *et al.* 1982). In *Hadronomus* the protolophid is also constricted relative to the hypolophid, but the nature of the compression, by lingual migration of the protolophid, is not apparent, nor is the trigonid as narrow or low, relative to the talonid.

Balbarines retain a small paraconid on the lingual margin of the anterior cingulum of M_2. In *Hadronomus* a lingual emargination of the anterior cingulum results in an accentuated bulge of the cingulum in about the same position as the paraconid in *Balbaroo*, but to align these forms on the basis of such uncertain resemblances is like buying a lottery ticket. *Hadronomus* differs from *Balbaroo* in having a well-developed anterior cingulum and a poorly developed posterior cingulum. In *Balbaroo* the posterior cingulum of M_2 is prominent and broad (Flannery *et al.* 1982). The same area in *Hadronomus* is represented by a large bulge which protrudes out over the posterior root of the hypolophid in lateral view (Woodburne 1967). Moreover, the lophs of *Balbaroo* are stouter, less tapered towards their apices, the enamel is relatively thicker and the buccal cingulum is broadly continuous across the midvalley. If *Hadronomus* were directly related to *Balbaroo*, some of

these very distinctive features should be in evidence.

The lower molars of *Galanarla tessellata* show a closer overall resemblance to those of *Hadronomus*, particularly in the proportions of the lophs, development and shape of the anterior cingulae, broad interloph valleys and less prominent buccal cingulum. The lower incisor alveolus on the dentary is distinctively stepped above the emergence of the root as in *Hadronomus*, and the I_1 is long-rooted, straight, lanceolate-crowned and lacks enamel on the lingual side. However, like *Balbaroo*, *Galanarla* has a large, distinct posterior cingulum.

The unassigned upper molars (Fig. 8E-F in Flannery *et al.* 1982) differ from *Hadronomus* in having a slight sinuosity of the lophs, relatively lower lophs and shorter, narrower anterior cingulae. They otherwise share the distinctive double crest which blocks the labial side of the interloph valley, a wide interloph valley and the presence of a post-link. The unassigned macropodid upper molars could have given rise to *Hadronomus* by slight suppression of the post-link and with a slight reduction of the width of the labial sulcus dividing the postparaconal crest and the buccal cingulum.

CONCLUSIONS

Although inconclusive, these various similarities tend to align *Hadronomus* with the more archaic macropodids; implying that the subfamilially unassigned mid-Miocene macropodid taxa, *Galanarla* and gen. et sp. unnamed (Flannery *et al.* 1982:229) are more closely related to *Hadronomus* than *Hadronomus* is to the sthenurines. The balbarines are generally similar but have no synapomorphies with *Hadronomus*. *Galanarla* is somewhat more sthenurine-like in having a curved molar row (macropodines tend to have fairly straight or excurvate lower molar rows), but with its distinctly potoroid-like offset of the premolar roots, a direct relationship is highly unlikely.

As there are no crania assigned to these forms, the wider systematic observations made here do not result from the primary consideration of this paper. However, the cranium of *Hadronomus* on its own has demonstrated that the genus is no closer to sthenurines than its dentition indicates, indeed it strongly reinforces the long-standing reservations about its relationship to any of the derived macropodids expressed originally by Woodburne (1967) and subsequently by Flannery (1983). Consequently, it has been concluded that *Hadronomus* is a representative of a distinct group of primitive macropodids that became extinct at the end of the Miocene.

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REDESCRIPTION OF THE BURROWING SPONGE *ZYZZYA MASSALIS* (DENDY) FROM THE SEYCHELLES AND HOUTMAN-ABROLHOS ISLANDS.

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ABSTRACT

Massive, burrowing, fistule-bearing specimens of *Zyzzya massalis* (Dendy) are described from the shallow subtidal of the Seychelles Islands, Indian Ocean, and Houtman-Abrolhos Islands, Western Australia. This material represents only the second occurrence of massive morphs of this species, whereas all other records since the original description have dealt with thinly encrusting morphs. The species is also the first record for Australian waters, which now confirms its circum-Indian Ocean distribution. It is referred to the family Coelosphàeridae, and acquires the nominal species *Paracornulum atoxa* Vacelet *et al.* as a new synonym.

KEYWORDS: *Zyzzya massalis, Plocamia, Damirina*, Poecilosclerida, Coelosphaeridae, Porifera, marine sponges, Seychelles Islands, Houtman-Abrolhos Islands.

INTRODUCTION

Recent collections of marine sponges by the USSR Research Vessel *Akademik Oparin* in the western and eastern Indian Ocean produced specimens of a burrowing sponge originally described as *Plocamia massalis* Dendy, and previously known only from deeper waters off Zanzibar (113 m depth), Mauritius (200 m depth), the Seychelles (unknown depth), and also recently collected from Three Kings Island, New Zealand (55-110 m depth). Material redescribed here from subtidal waters of the Seychelles (20 m depth) and Houtman-Abrolhos Islands (18 m depth) represents only the second occasion in which the massive (? adult) growth form of the species has been collected. It is also the first time that the species has been recorded in Australian waters. There are several papers describing marine sponges from the Seychelles Islands (Wright 1881; Ridley 1884; Topsent 1893; Dendy 1916, 1922; Thomas 1973), but only one work pertaining to the Houtman-Abrolhos Islands sponge fauna (containing 48 species; Dendy and Frederick 1924).

The Director of the Pacific Institute of Bio-organic Chemistry, Professor Georgy Elyakov, and the scientists and crew of the RV *Akademik Oparin* are gratefully acknowledged for providing the senior author with an opportunity to visit and collect from various remote reefs along the western and northwestern coast of Australia. Grants from the Sir Winston Churchill Memorial Trust and Australian Biological Resources Survey which enabled the senior author access to European collections are gratefully acknowledged, as are Miss Shirley Stone and Prof. Claude Lévi for providing access to their collections in London and Paris Museums, respectively. The following abbreviations are used in the text: BMNH, British Museum (Natural History), London; NTM, Northern Territory Museum, Darwin; MNHN LBIM, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Muséum National d'Histoire Naturelle, Paris; PIBOC, Pacific Institute of Bio-organic Chemistry, Vladivostok. Methods of spicule preparation for light and scanning electron microscopy are described elsewhere (Hooper 1986).

SYSTEMATICS

Family Coelosphaeridae Hentschel

Coelosphaeridae Hentschel, 1923:102.
Cornulidae Lévi and Lévi, 1983:966.

Diagnosis. Poecilosclerida with excavating, burrowing or cryptic habits, and with specialized hollow, fistulose aquiferous systems. Skeleton usually consists of well differentiated (in structure or spicule composition, or both) ectosomal and choanosomal regions, both composed of diactinal megascleres (tylotes, strongyles, oxeas, or modifications), and which may form a tangential ectosomal crust. Microscleres may include arcuate and palmate isochelae, palmate anisochelae, sigmata, toxa and raphides.

Genus *Zyzzya* de Laubenfels

Zyzzya de Laubenfels, 1936:64 (type species *Plocamia massalis* Dendy, 1922:78, by original designation and monotypy).

Damirina Burton, 1959:240 (type species *Damirina verticillata* Burton, 1959:240, by original designation and monotypy).

Diagnosis. Coelosphaerids with verticillate-spined strongyles. Massive burrowing or cryptic encrusting growth form, with solid apical fistules or blind papillae. Ectosome consists of a thick detachable crust of tangentially orientated tylotes bearing microspined heads. Choanosomal skeleton contains irregular, widely-spaced multispicular tracts of tylotes ascending to the surface, between which is dispersed an irregular isodictyal reticulation of verticillately-spined strongyles. Microscleres, if present, are palmate isochelae.

Zyzzya massalis (Dendy)
(Figs 1-6)

Plocamia massalis Dendy, 1922:78-79, pl.14, fig. 5a-e.

Dendoricella massalis - Topsent 1928:64.

Lissodendoryx massalis - Burton 1935:400; Thomas 1973:32-33, pl.2, fig.4.

Zyzzya massalis - de Laubenfels 1936:64.

Zyzza massalis - Bergquist and Fromont 1988:56-57, pl. 23F.

Damirina verticillata Burton, 1959: 240-241, text-fig. 25.

Paracornulum atoxa Vacelet, Vasseur and Lévi, 1976:59-60, text-fig.38.

Fig. 1. *Zyzzya massalis*: Houtman-Abrolhos Islands specimen (NTM Z2891).

Type material. HOLOTYPE - BMNH 1921.11.7.67 (only fragment remains): Off Mauritius, Indian Ocean, 200m depth, 23 August 1905. Coll. Percy Sladen Trust Expedition, HMS *Sealark*, dredge. HOLOTYPE of *D. verticillata* - BMNH 1936.3.4.510: Pemba Channel, off Tanga, Zanzibar, 05° 04.9'S, 30° 13.2'E, 113m depth, 15 January 1934. Coll. John Murray Expedition, stn. 112, dredge. SCHIZOTYPE of *P. atoxa* - MNHN LBIM DJV 46: Sud Grande Passe d'Ifaty, off Tuléar, Madagascar, 5.5m depth. Coll. P. Vasseur, SCUBA.

Additional material. NTM Z2891 (fragment PIBOC): Base of an outer fringing *Acropora* reef, eastern side of Pelsart Islets, Houtman-Abrolhos Islands, Western Australia, 28° 51.6'S, 113° 52.5'E, 18-20m depth. Coll. J.N.A. Hooper, SCUBA, RV *Akademik Oparin*, 09 July 1987, stn. HA1 (no.48). PIBOC 04-216 (fragment only) (plus fragment in NTM): Northwest side of outer coral reef, D'Arros Islands, Seychelles Republic, 05° 24.47'S, 53° 19.14'E, 12-20m depth. Coll.

Alexsandr Katancev, SCUBA, RV *Akademik Oparin*, stn.38, April 1987.

Description. Shape: (2891) Subspherical (now cut in half), with at least one third of the base lying in a shallow burrow in soft sediment. The surface of the sponge in the basal region has embedded fragments of dead coral and rock; the upper surface tapers to a single short fistule at the apex, with a terminal sieve-plate of oscula; (216) fragment of massive subspherical sponge with a smooth detachable ectosome; fistules, if they were present, are now not intact.

Dimensions: (2891) 140 mm high from base to the apex of the fistule, 84 mm diameter at the base of the sponge; 75 mm diameter near the fistular constriction; fistule is 38 mm high and 31 mm diameter, of solid construction.

Oscula: Sieve-plate at the apex of the fistule is comprised of up to 10 exhalant pores, from 1-2 mm in diameter. No ostial pores were seen on the basal section.

Colour: Live colouration is dark brown (Munsell 10R 5/2), which fades slightly to grey-brown in ethanol.

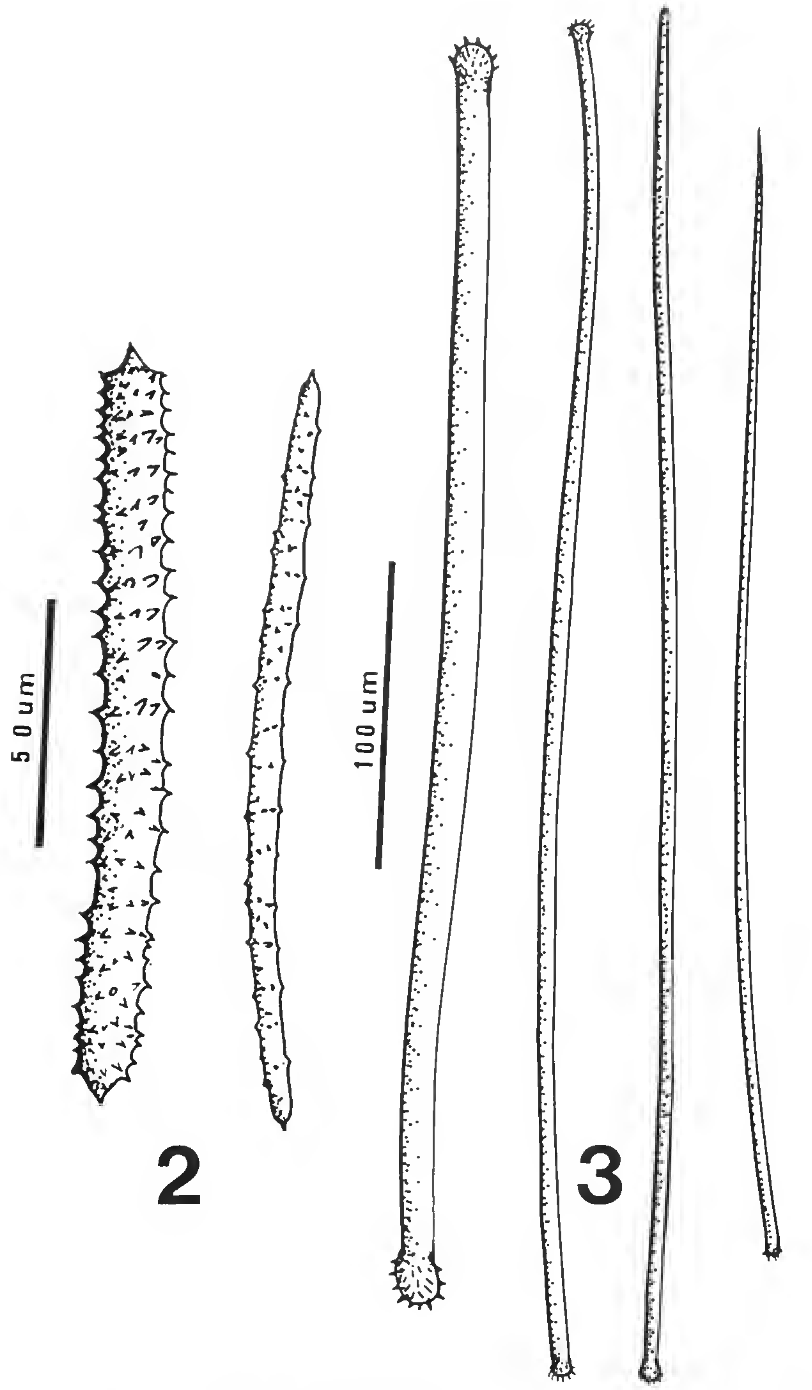
Texture: Sponge consistency is firm but compressible.

Ectosome: The surface is optically smooth, with a distinct skin-like covering which is detachable and easily damaged in preserved material. The ectosomal skeleton consists of a tangential layer of tylotes, through which are dispersed irregular paratangential tracts of acanthostrongyles. Spongin in the ectosomal region is relatively sparse, and slightly darker pigmented than in the deeper choanosomal region.

Choanosome: The choanosomal skeleton contains conspicuous plumose multispicular tracts of tylotes (90-230 µm in diameter), which meander, anastomose, sometimes form wide meshed reticulations (mesh sizes 240-650 µm), and vaguely ascend to the surface. Dispersed between these widely spaced tracts is an irregular unispicular subisodictyal reticulation of acanthostrongyles and occasional larger tylotes. In the choanosomal region of the fistule, juvenile raphidiform tylotes as well as mature examples are very abundant and dispersed between the acanthostrongyles, whereas in the choanosomal region of the base of the sponge the isodictyal reticulation of acanthostrongyles is much more dense. Spongin in the mesohyl is very heavy, dark brown pigmented and collagenous. Exhalant canals of the aquiferous system are elliptical, between 190x130 and 2350 x 640 µm in dimension. Choanocyte chambers are difficult to discern due to the heavy mesohyl spongin and dispersed spiculation, vaguely oval in shape and between 30-110 µm in diameter.

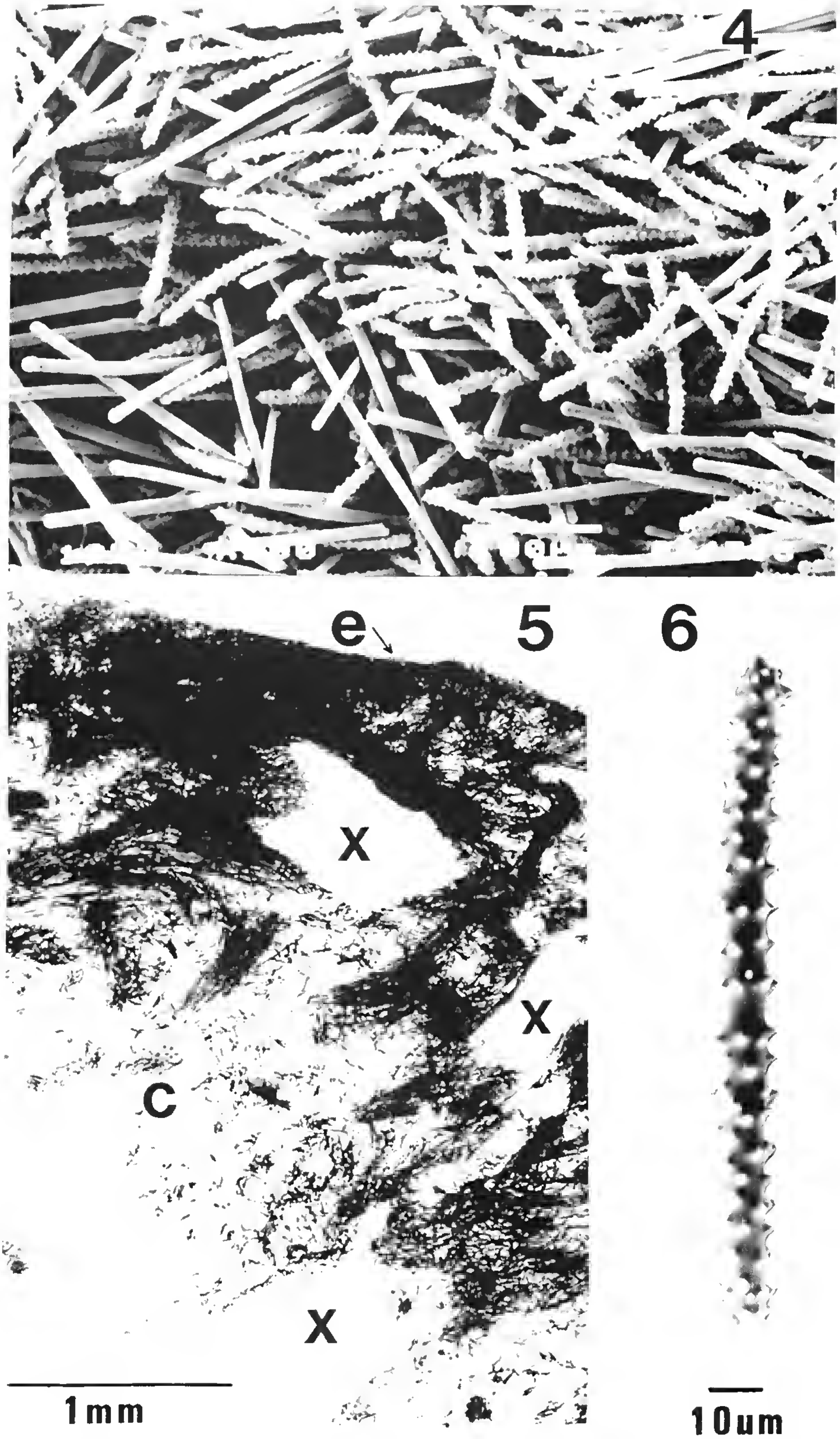
Table 1. Comparison between morphological features and spicule dimensions for specimens of *Zyzzya massalis*. Measurements are given in µm, and shown as range (and mean).

	Plocamia massalis Dendy 1922	*Damirina verticillata* Burton 1959	*Lissodendoryx massalis* (Thomas 1973)	*Zyzzya massalis* (Bergquist and Fromont 1988)	*Paracornulum atoxa* Vacelet et al. 1976	*Zyzzya massalis* (NTM Z2891)	*Zyzzya massalis* (PIBOC 04-216
Source	BMNH 1921.11.7.67	BMNH 1936.3.4.510	(fromThomas 1973)	(from Bergquist and Fromont 1988)	MNHN LBIM DJ46	present material	present material
Growth form	massive subspherical	encrusting in dead coral	thinly encrusting	thinly encrusting	encrusting and excavating dead coral	massive subspherical	probably massive
Colour	dark chocolate brown	dark brown	dark brown	dark red brown	brown	dark brown	brown
Fistules	short, apical, hollow	hollow	absent	absent	long, hollow	single solid, apical seive plate	(not seen)
Choanosome skeleton	dispersed multispicular tracts, and dense subisodictyal unispicular mesh	unispicular subisodictyal mesh	few tracts mainly confused isodictyal mesh	unispicular isodictyal reticulation, dense near the base	confused unispicular isodictyal	dispersed multispicular tracts, dense subisodictyal mesh	multispicular tracts, and confused subisodictyal mesh
Amphitylotes (apices)	286-(363.3)-408 x 6-(9.4)-14 (spined, some asymmetrical)	298-(374.4)-468 x 5-(11.5)-15 (spined)	222-260x4 (spined)	367-(385)-402 x 6-(9)-12 (spined)	180-(408.6)-590 x 2-(12.5)-20 (spined, some asymmetrical)	280-(381.1)-438 x 1.5-(8.2)-12 (spined, some asymmetrical)	305-(364.4)-418 x 3-(9.2)-12 (spined, some asymmetrical)
Acanthostrongyles	155-(171.0)-232 x 4-(10.8)-15	134-(193.5)-256 x 5-(16.1)-20	105-142x6	217-(241)-266 x 11-(12)-14	109-(209.1)-285 x 3-(11.8)-15	118-(162.2)-190 x 4-(11.1)-14	148-(197.7)-242 x 5-(12.2)-15
Palmate isochelae	14-(16.9)-20	absent	16	15-(16)-16	12-(17.0)-22	absent	absent
Locality	Mauritius	Zanzibar	Seychelles	New Zealand	Madagascar	Houtman-Abrolhos	Seychelles
Depth	200m	113m	unknown	55-110m	5.5m	18-20m	12-20m



Figs 2-3. *Zyzzya massalis*: **2**, verticillate acanthostrongyles, adult and juvenile form; **3**; tylotes, including styloid modifications of juvenile forms.

Megascleres: Tylotes are long, slender, often slightly curved, occasionally sinuous, with moderate tylote swellings at either end; larger spicules invariably have microspined heads. Juvenile forms occur also, ranging from much more slender varieties of the larger spicules, often with asymmetrical ends, to very thin raphidiform spicules with styloid modifications. Acanthostrongyles are generally symmetrically curved from the centre, with oxeote modifications in the form of a single terminal spine at each end, and with relatively even verticillate spination along the shaft, although juvenile forms of these spicules also



Figs 4-6. *Zyzzya massalis:* **4,** SEM tangential view of ectosomal skeleton; **5,** light micrograph of cross-section through fistule region (**c,** choanosomal region, **e,** ectosomal skeleton, **x,** exhalant canals); **6,** SEM of verticillate acanthostrongyle.

occur which have only vestigial spination. Refer to Table 1 for dimensions.

Microscleres: Absent.

Remarks. Both the Seychelles and Houtman-Abrolhos Islands material examined here lack microscleres. Furthermore, it was confirmed from a re-examination of Burton's (1959) holotype of *D. verticillata* that his observations were indeed correct: that his specimen also lacked isochelae microscleres, and these spicules were not merely overlooked as supposed by Bergquist and Fromont (1988). This infers that the species is prone to shedding its microscleres, since they are absent in 3 of the 7 specimens known so far. However, for the Poecilosclerida this observation is not unique (van Soest 1984), and certainly not an important criterion for differentiating the genera *Damirina* and *Zyzzya* (cf. Bergquist and Fromont 1988).

The precise gross-morphological details of the Seychelles specimen (216) is not known, since soon after collection it was divided up to provide material for biochemical analysis, microbiological assays, as well as a voucher specimen. However, from what remained of this specimen it was obvious that fragments came from a massive and not an encrusting specimen. (Similarly, only one half of the original Houtman-Abrolhos Islands material is now extant, the other portion was frozen and subsequently used for marine natural products investigations). Thus, the species appears to be relatively polymorphic in growth form, ranging from cryptic excavating to massive burrowing forms.

Three nominal species have been referred to *Zyzzya*: *Plocamia massalis*, *Paracornulum atoxa* Vacelet *et al.* and *Damirina verticillata* Burton. All three species have identical spicule geometry, including verticillately- spined acanthostrongyles. Skeletal construction is comparable also, despite the fact that *P. atoxa* and *D. verticillata* are only known from encrusting specimens. Contrary to arguments presented by Bergquist and Fromont (1988), all three species do have comparable and overlapping spicule dimensions (Table 1), and all have peculiar oxeote modifications to at least some of the acanthostrongyles (usually in the form of a single large spine at each end of the spicule). These features were noted from re-examination of type material. Bergquist and Fromont (1988) synonymised *D. verticillata* with the present species, and it is proposed here to merge *P. atoxa* with *Zyzzya massalis* also. The present record of the species from the Houtman-Abrolhos Islands confirms that the species has an oceanic-island, circum-Indian Ocean distribution, with a relatively extensive bathymetric range (5.5-200 m). The verticillately-spined acanthostrongyles present in *Zyzzya* are reminiscent of those seen in *Agelas* in particular (order Axinellida), but the two genera are not necessarily closely related in any other features.

Lévi and Lévi (1983) created the family Cornulidae for coelosphaerid sponges which have palmate isochelae microscleres, and this taxon has been recognised subsequently by Bergquist and Fromont (1988). Those authors are not followed here, since the criterion of whether isochelae microscleres are palmate, arcuate, birotulate or absent (presumably secondarily lost) cannot be considered to be of sufficient systematic importance at the family level of classification. This position is consistent with a similar treatment of other Poecilosclerida families (e.g. van Soest 1984; Hooper 1989, in press).

Nominal genera referred to Cornulidae by authors are: *Achelidernia* Topsent, *Astylinifer* Topsent, *Coelocarteria* Burton (including *Ichnodonax* de Laubenfels), *Cornulum* Dendy (including *Coelosphaerella* de Laubenfels, and *Cornulella* Dendy), *Cornulotrocha* Topsent, *Fusifer* Dendy, *Heterocornulum* Lévi and Lévi, *Paracornulum* Hallmann (including *Cornulacantha* Lévi), and *Zyzzya* de Laubenfels (including *Damirina* Burton). The family Coelosphaeridae *sensu* Bergquist and Fromont (1988) contains taxa otherwise similar to Cornulidae, but with isochelae that are not palmate. Genera included with this group by authors are: *Amphiastrella* Dendy (including *Xytopsene* de Laubenfels), *Coelodischela* Vacelet *et al.*, *Coelosphaera* Wyville Thomson (including *Coelosphaericon* Bakus, *Histoderma* Carter, and *Sideroderniella* Dendy), *Damiria* Keller, *Histodermella* Lundbeck (including *Hiltonus* de Laubenfels, and *Histodermopsis* de Laubenfels), *Histodermion* Topsent, *Inflatella* Schmidt (including *Joyeuxia* Topsent), *Lepidosphaera* Lévi and Lévi, *Manawa* Bergquist and Fromont, *Phlyctaenopora* Topsent, and *Pyloderma* Kirkpatrick (including *Sideroderma sensu* Ridley and Dendy). Most of these genera, in

both nominal family groups should be re-united in a single family, Coelosphaeridae, although some are very closely related, possibly synonyms (e.g. *Pyloderma* may be a junior synonym of *Coelosphaera* (van Soest 1984), *Coelodischela* is close to *Guitarra* and *Tetrapocillon* (van Soest 1988)), some may be more closely related to the Myxillidae (e.g. *Histodermion*, *Paracornulum*) or Mycalidae (e.g. *Phlyctaenopora*), and others do not fit with the coelosphaerids at all (e.g. *Cornulotrocha*, *Astylinifer*).

The coelosphaerids as defined here appear to be relatively homogeneous, on the basis of their gross morphology and spiculation. The family contains taxa which typically have a fistulous aquiferous system, but it is likely that this fistulose habit is related to an ecological specialization for burrowing or excavating the substrate (van Soest 1984). This character is certainly not unique amongst the Demospongiae, and it is obvious that this specialisation has arisen independently in several other groups also (some Haplosclerida such as *Oceanapia*, *Siphonodictyon*; Hadromerida such as *Polymastia*, *Spirastrella*; Halichondriida such as *Ciocalypta*; Astrophorida such as *Monsyringia*, *Disyringia*; Bergquist and Fromont 1988). Consequently, van Soest (1984) proposed that the possession of fistules could not be used to define a phylogenetically useful family taxon, since it is not unique for the group. He tentatively suggested that most of the genera could fit with the Myxillidae. However, the gross morphological comparison between the fistules of the Coelosphaeridae and other groups may be misleading, when significant differences may exist in microstructure and spiculation (Bergquist and Fromont 1988). It is proposed here to retain the coelosphaerid family taxon, because this group of burrowing and excavating fistulose sponges appears to be monophyletic, on the basis of spiculation and skeletal evidence at least, although it is admitted that no unique discriminating characters are present other than the gross morphology.

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THREE SPECIES OF ISOPODA BOPYRIDAE NEW TO THE FAUNA OF THE PHILIPPINES

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ABSTRACT

Palaemonellione cebuensis gen. et sp. nov. is described as a parasite of the palaemonid shrimp *Palaemonella pottsi* (Borradaile) from Cebu, Philippines. The new genus is closely similar to *Probopyrus* Giard and Bonnier. *Allokepon sinensis* (Danforth 1972) is reported for the first time from the Philippines as a parasite of the portunid crab *Portunus pelagicus* (Linnaeus), a host previously recorded for this parasite elsewhere. The single female is the first immature one of *A. sinensis* known. *Diplophryxus gracilis* sp. nov. is described as a parasite of the palaemonid shrimp *Urocaridella gracilis* Borradaile (?).

KEYWORDS: Crustacea, decapoda, Isopoda, Bopyridae, *Palaemonellione cebuensis*, *Allokepon sinensis*, *Diplophryxus gracilis*, new genera, new species, parasites, Philippines.

INTRODUCTION

The fauna of Isopoda Bopyridae of the Philippines is only poorly known, whereas it would be expected to be very large because of that archipelago's location in the tropical western Pacific Ocean. Semper (1881) described *Bopyrus* (now *Probopyrus*) *ascendens*, the first bopyrid ever recorded in freshwater, from a Philippine mountain stream. Richardson (1910) recorded nine additional species from the Philippines, all but two described as new. Nierstrasz and Brender à Brandis (1929, 1931) added four species, two of them newly described. Bourdon (1976, 1981) reported eight species previously unknown from the Philippines, including three described as new to science. Finally, Palisoc (1987) added one more species to that fauna. Other scattered reports also cite the Philippine occurrence of four more unidentified species, some of which are probably undescribed. Recently, specimens of three more species of Philippine bopyrids in various museum collections have become available for study; one represents a new genus and species, one a new species in an existing genus, and one a new geographical record. Thus the number of named bopyrid species known from the Philippines now stands at 26, of which 15 claim that archipelago as type-locality. Because that number is probably far short of the number of species actually occurring there, it is too early to present a key to (or even a list of) Philippine species, which would be expected to become quickly obsolete.

SYSTEMATICS

Family Bopyridae Rafinesque
Subfamily Bopyrinae Rafinesque
Palaemonellione gen. nov.

Type-species. *Palaemonellione cebuensis* sp. nov.

Diagnosis. Female: Body only moderately distorted. Head completely separated from pereon and somewhat extending out from it; maxilliped with articles deeply separated, palp articulating and consisting of two partly fused articles. Pereomeres all distinct and misaligned laterally, each slightly indented on both sides; oostegites completely surrounding but not covering brood pouch, all heavily pigmented; first oostegite without internal ornamentation or posterolateral point; pereopods doubling in size posteriorly. Pleomeres medially fused but distinct laterally and posteriorly; pleopods uniramous flaps, only on long side; no uropods.

Male: Body over three times as long as wide. Head fused with pereon except at sides. Pereomeres distinct; pereopods relatively large, all about same size, all with meri and carpi fused, dactyli progressively smaller

posteriorly. Pleon set off from final pereomere and narrower than it, rather long and subrectangular, completely lacking appendages.

Host: In palaemonid genus *Palaemonella*.

Etymology: derived from generic name of known host, *Palaemonella* + bopyrid generic name *Ione*. Gender feminine.

Palaemonellione cebuensis sp. nov.
(Figs 1, 2)

Type Material. Infesting *Palaemonella pottsi* (Borradaile), A. J. Bruce, det. of host. Moalboal, Cebu, Philippines, March/April 1983, V. Storch coll. #97. 1 female, holotype; 1 male, allotype, Northern Territory Museum, NTM Cr. 006489.

Description. Female holotype (Fig. 1). Length 2.6 mm, maximal width 1.7 mm, head length 0.5 mm, head width 0.7 mm, pleon length 0.9 mm. Body axis distortion 72°. All body regions distinct (Fig. 1A, B).

Posterior margin nearly semicircular, slightly extended from pereon. Short frontal lamina reaching clear across front of head but not along sides. Irregularly slit-shaped eyes medially placed. Antennae 1 and 2 (Fig. 1C) of 3 and 4 articles, respectively, all but basal articles distally somewhat setose. Maxilliped (Fig. 1D) suboval, its segments deeply separated, posterior one smaller; large, articulating palp (Fig. 1E) arising from anteromedial corner, incompletely 2-segmented, nonsetose; plectron (Fig. 1F) sharply pointed, arched forward. Barbula indiscernible.

All pereomeres distinct, their lateral margins forming irregular outline, nearly all more or less subdivided laterally. Oostegites completely surrounding brood pouch and covering all but middle portion of ventral surface of pereon; first oostegite (Fig. 1G) irregularly rounded both anteriorly and posteriorly, posterior segment broader but shorter, internal ridge unadorned, posterolateral point completely absent; fifth oostegites much longer than others, extending far posteriorly and partly covering pleon. Pereopods (Fig. 1I, J) of about constant proportions but doubling in size posteriorly; all meri and carpi with setose anterior margins, some fused into single article, others separate.

Pleon (Fig. 1K) medially fused, but five pleomeres separated laterally; first two pleomeres on short side extending as slender flaps. Three uniramous flaplike pleopods on long side, none on short side. No uropods.

Male allotype (Fig. 2). - Length 0.96mm, maximal width 0.30mm, head length 0.15mm, head width 0.21mm, pleon length 0.25mm, pleon width 0.21mm. Head and first pereomere fused, but all other body segments distinct (Fig. 2A,B).

Head nearly as wide as first pereomere, extending prominently forward from it. Large fairly faint kidney-shaped eyes near posterolateral borders. Antennae 1 and 2 (Fig. 2C,D) of 3 and 4 articles, respectively, first one with all articles setose, second one with setae only terminally; basal segment of antenna 2 perpendicular to others.

Sides of pereon subparallel, pereomeres not deeply separated laterally. Pereopods (Fig. 2E,F) all of nearly same size, though bases progressively larger and dactyli progressively smaller posteriorly; all carpi and meri fused with slight indentation indicating lost segmentation.

Pleon abruptly narrower than pereon, completely fused into single piece, broadly triangular in outline. All appendages absent, but paired tufts of minute setae (Fig. 2G) on slightly raised posteroventral region indicating traces of lost uropods.

Etymology. The specific name *cebuensis* refers to the type-locality, Cebu Island, the Philippines.

Remarks. Heretofore, branchially infesting bopyrids (all in the subfamily Bopyrinae) belonging to four different genera have been recorded as parasites of shrimps of the family Palaemonidae. The most numerous of these occur in the genus *Probopyrus*, the others belonging to *Schizobopyrina* (of which many species have been recorded as members of *Bopyrina*), *Bopyrus*, *Allobopyrus* and *Probynia*. *Palaemonellione* resembles all of these genera in some particulars but also differs significantly from each. In general shape and pigmentation of the oostegites, the female of *P. cebuensis* closely resembles those of *Pobopyrus*; females of *Probopyrus* differ in having nonarticulating maxilliped palps, strongly pointed first oostegites and all pleomeres distinct on both sides; males of *Probopyrus* have all pereopodal articles present, distinct pleomeres and at least traces of pleopods (Markham 1985a). Females of

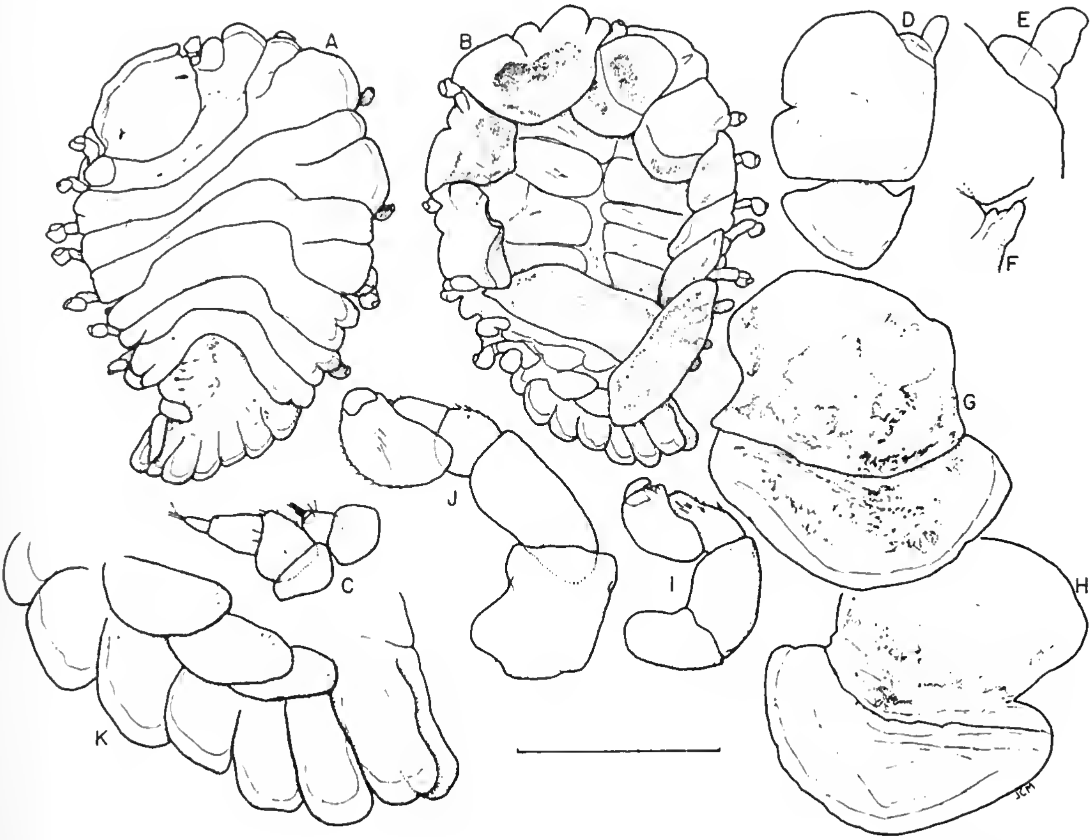

Fig. 1. *Palaemonellione cebuensis*, holotype female: A, dorsal view; B, ventral view; C, right antennae; D, right maxilliped; E, palp of same; F, plectron of same; G, right oostegite 1, external view; H, same, internal view; I, right pereopod 1; J, right pereopod 7; K, pleon, ventral view. Scaleline: 1.1mm for A, B; 0.4mm for D, G, H, K; 0.2mm for C, E, F, I, J.

Schizobopyrina have dimorphic first oostegites with long posterolateral points and completely distinct pleomeres; males of that genus have lateral indications of four pleomeres and at least traces of pleopods (Markham 1985a). Females of *Bopyrus* differ from that of *Palaemonellione* in the same way as those of *Probopyrus*, while males of *Bopyrus* have pleomeres distinct or at least laterally indicated and pleopods present (Bourdon 1968). The female of *Allobopyrus* differs from that of *Palaemonellione* in the same ways as those of *Probopyrus* and also has biramous pleopods; the male of *Allobopyrus* is unknown (Bourdon and Bruce 1983). The female of *Probynia* is much more distorted; further, it and its male both differ from those of *Palaemonellione* in the same ways as both sexes of *Probopyrus* (Bourdon and Bruce 1983). Among genera whose species do not infest palaemonids, *Bopyrina* is closely similar in that its females have asymmetrically fused pleons, but their maxillipeds lack palps, their first oostegites are dimorphic and elongate, the other oostegites are greatly reduced, and pleopods are nearly similar on both sides; males of *Bopyrina* are similar to those of *Palaemonellione* in having heads and pereons fused and no pleopods, but their elongate pleons are divided into some pleomeres (Markham 1985a). In the genus *Bopyroides*, females have much reduced maxillipedal palps and clearly demarcated pleomeres completely lacking appendages, while the males have separated heads (Bourdon 1968). Finally, in *Palaemonellione*, the asymmetry of the female's pleopods set it off from all other genera.

Although no species of *Palaemonella* has previously been reported branchially infested

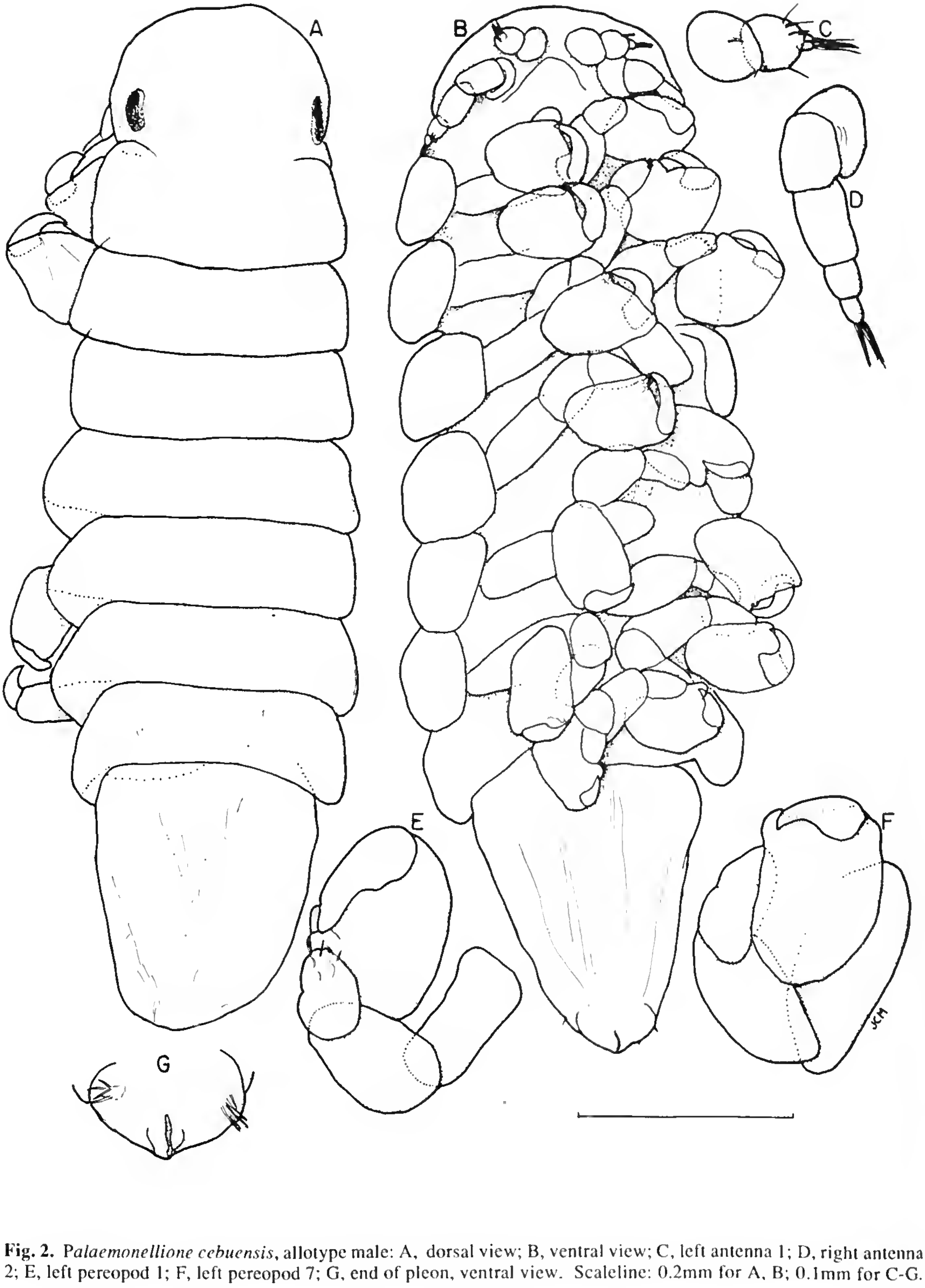

Fig. 2. *Palaemonellione cebuensis*, allotype male: A, dorsal view; B, ventral view; C, left antenna 1; D, right antenna 2; E, left pereopod 1; F, left pereopod 7; G, end of pleon, ventral view. Scaleline: 0.2mm for A, B; 0.1mm for C-G.

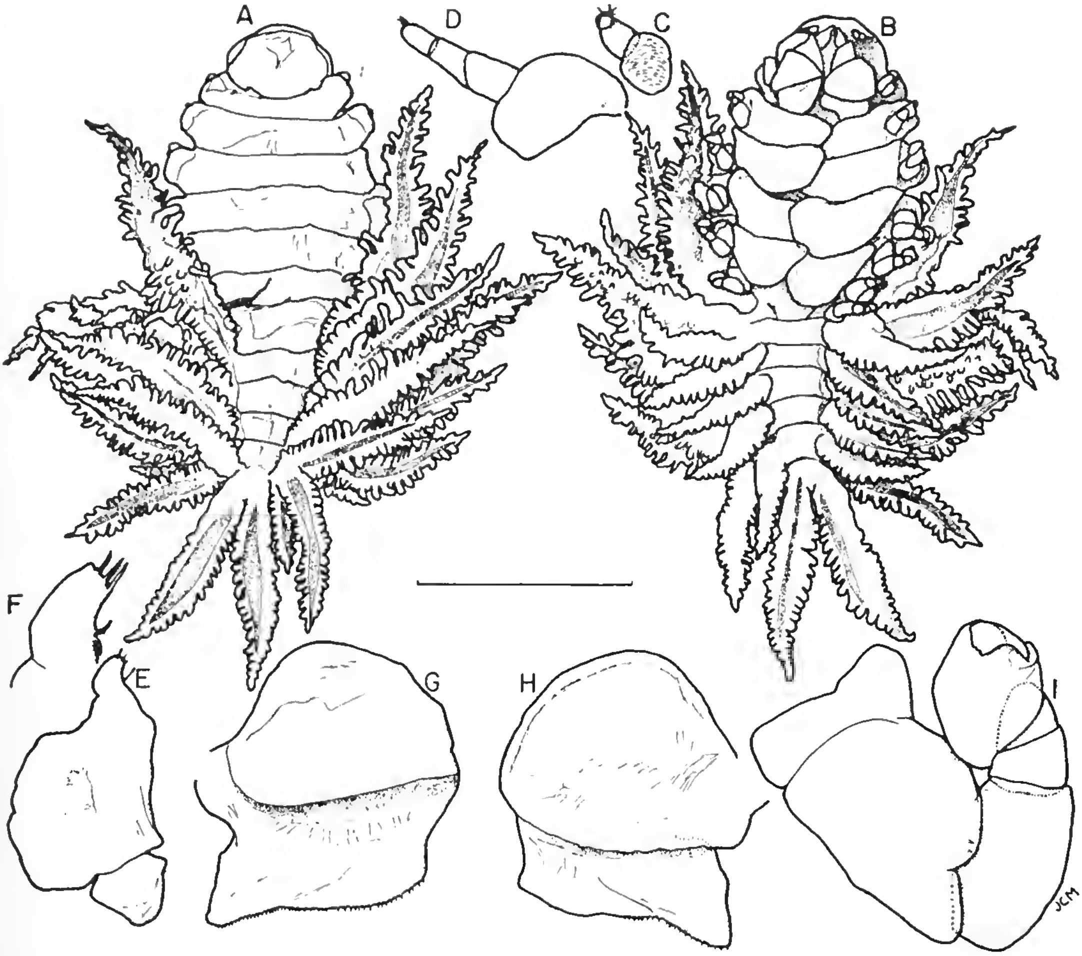

Fig. 3. *Allokepon sinensis*, immature female: A, dorsal view; B, ventral view; C, right antenna 1; D, right antenna 2; E, left maxilliped; F, palp of same; G, right oostegite 1, external view; H, same, internal view; I, right pereopod 1. Scaleline: 4.0mm for A, B; 0.9mm for E, G, H; 0.3mm for C, D, F, I.

by a bopyrid, *P. rotumana* Borradaile is known to bear the abdominally infesting (Subfamily Hemiarthrinae) species *Metaphrixus intutus* Bruce in Singapore (Bruce 1979) and northwestern Australia (Bruce 1986), while *P. vestigialis* Kemp is recorded as host of the same species in Zanzibar (Bruce 1965). This is thus the first record of bopyrid infestation of *P. pottsi*.

Subfamily Ioninae H. Milne Edwards
Allokepon sinensis (Danforth)
(Fig. 3)

Grapsicepon sinensis Danforth, 1972:163-167, Fig. 1 (Hong Kong; infesting portunid crab *Lissocarcinus orbicularis* Dana).

Allokepon sinensis - Markham 1982:357-359, 385, Fig. 19 (Redescription of holotype female; reassignment to *Allokepon*, gen. nov.); Markham 1985b:3, 38-40, 63, Figs. 18-19; Table 1 (Phuket, Thailand; infesting portunid crab *Portunus pelagicus* (Linnaeus); redescription of male).

Material. Infesting *Portunus pelagicus* (Linnaeus), J. S. Garth, det. of host. From unrecorded locality, Philippines. 1 immature female, California Academy of Sciences.

Descriptive notes. Body length (exclusive of appendages) 3.0mm, maximal body width 1.4mm, head length 0.4mm, pleon length 1.0mm. Body axis distortion 14°.

Similar to mature females previously seen, except: body smaller and proportionately much narrower; middorsal bosses greatly reduced and very difficult to discern (and not visible in drawing) though two present; ooste-

gites not quite covering pereon ventrally; pleopods relatively large and extended.

Remarks. All of the differences from other specimens cited above seem attributable to the immaturity (as indicated by the absence of a male, the complete lack of eggs and the small size) of this female. It is especially noteworthy that the middorsal pleonal bosses are markedly underdeveloped, because the number and structure of those bosses are important characters for the definition of *Allokepon* and allied genera; thus it is valuable to know that they become conspicuous only with maturity. In the present case, identification was difficult until the host was identified and served as a guide. The particular structures of the maxilliped, first oostegite and pereopods, all illustrated, conform closely enough with those previously known to confirm the identification.

This is the first record of *Allokepon sinensis* in the Philippines, but the present host, *Portunus pelagicus*, has previously been reported bearing it in Thailand (Markham 1985b).

Diplophryxus gracilis sp. nov.
(Figs 4, 5)

Type material. Infesting *Urocaridella gracilis* Borradaile (?), A. J. Bruce, det. of host. MUSORSTOM 3 "Coriolis" Station CP/142, Philippines, 11°47'N, 123°02'E, 26-27m, 6 June 1985. 1 female, holotype; 1 male, allotype, Muséum National d'Histoire Naturelle, Paris.

Description. Female holotype (Fig. 4). Length 2.6 mm, maximal width 1.4 mm, head length 0.6 mm, head width 0.4 mm, pleon length 1.4 mm. Double body axis distortion, head-pereon 80°, pereon-pleon 42°. Head distinct but pleon fused with pereon (Fig. 4A,B).

Hexagonal head deeply set into pereon, overreached by one oostegite and four pereopods. Middorsal surface grooved, probably containing minute antennae, though no antennae discernible. Maxilliped (Fig. 4C) elongate, with irregularly oblique anterolateral margin lacking palp and small triangular posterior article. Barbula indiscernible.

Pereon ovate, extending forward beyond head and backward over half of pleon. First oostegites (Fig. 4D-G) strongly dimorphic, enclosed in brood pouch; right one much reduced, its anterior article much larger than posterior one; left first oostegite with anterior article short and broad and posterior article long and slenderly pointed. Left oostegite 2 arching over front of body from ventral to dorsal region, its outer surface densely crenulate; oostegites 2-4 enclosing brood pouch but gaping slightly open. Only two pereopods on long (left) side, pressed against anterior margin of head, both reduced (Fig. 4H); first pereopod opposite (Fig. 4I) very long and prominently extending beyond anterior margin of body from in front of head; tiny pereopods 2-6 (Fig. 4J) on that side spaced along side of pereon, somewhat larger right pereopod 7 beneath pleon.

Pleon long and slender, arising from ventral region of pereon. Pleomeres fused except for slight separation posteriorly. Four pairs of biramous lateral plates and four pairs of similar biramous pleopods, their lanceolate flexible rami extending far beyond sides and end of pleon; some rami produced into slender points. Terminal bulbous pleomere (Fig. 4K) lacking appendages, produced into nipple-like posterior point.

Male allotype (Fig. 5). Length 0.5mm, maximal width 0.2mm, head length 0.1mm, head width 0.1mm, pleon length 0.2mm. All body segments distinct. Spots of pigment scattered on dorsal surface.

Head abruptly narrower than first pereomere, extending prominently forward from it. Large dark irregularly shaped eyes near posterolateral borders. Antennae too minute to distinguish.

Sides of pereon subparallel, but some pereomeres with markedly misaligned margins, pereomeres not deeply separated laterally. Pereopods too tiny for illustration, evidently all of nearly same size.

Pleon about as broad as pereon, completely fused into single piece, broadly triangular in outline. All appendages absent. Posterior margin produced into slightly separated knob.

Etymology. The specific name *gracilis*, meaning "slender" refers to the body outlines of both sexes and the pleon and pleonal appendages of the female; it also reflects the specific name of the only known host of the new species, the palaemonid shrimp *Urocaridella gracilis*.

Remarks. Worldwide, there are five other accepted species of diplophyxus; three of them infest *Alpheus* spp. (Family Alpheidae),

Fig. 4. *Diplophryxus gracilis*, holotype female: A, dorsal view; B, ventral view; C, right maxilliped; D, right oostegite 1, external view; E, same, internal view; F, left oostegite 1, external view; G, same, internal view; H, left pereopod 1; I, right pereopod 1; J, right pereopod 5; K, tip of pleon in dorsal view. Scaleline: 1.00mm for A, B; 0.56mm for C-G; 0.35mm for H-J; 0.18mm for K.

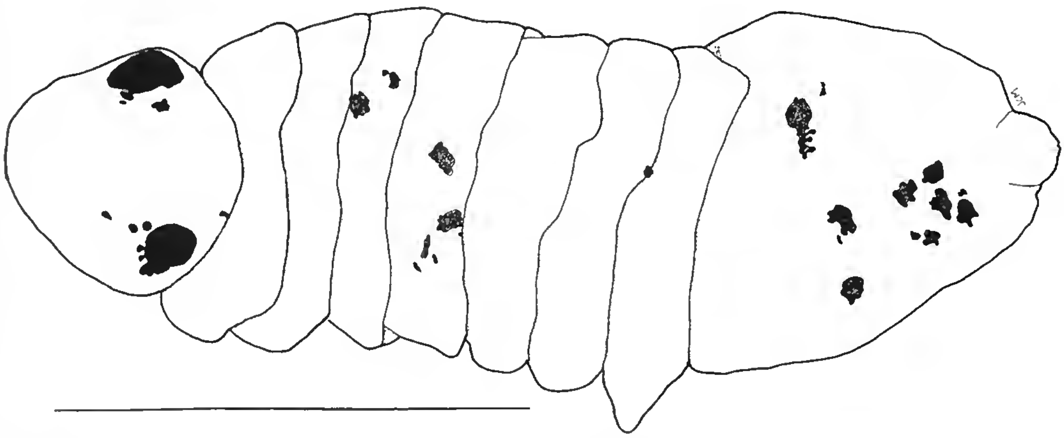

Fig. 5. *Diplophryxus gracilis*, allotype male in dorsal view. Scaleline: 0.2mm.

one infests a *Gnathophyllum* (Gnathophyllidae), and the other *Leander* spp. (Palaemonidae). All of the females, as well as that of *D. gracilis*, are immediately recognizable as members of *Diplophryxus* in having compound distortion, a dorsal groove on the head containing the antennae, one or both second oostegites extending over to the dorsal surface, only two complete pereopods on the the longer side and the pleopodal rami and lateral plates multidivided. Males of the genus are indistinguishible from those of several other hemiarthrine genera. Two characters which readily set off the female of *D. gracilis* from all others are the very slender central portion of its pleon and the bulbous terminal pleomere produced into a peculiar knob. The females of *D. jordani* Richardson from India, Japan and Thailand (Markham 1985b) and *D. siankaanensis* Markham from the northwestern Atlantic (Markham 1988) appear most similar to that of *D. gracilis*, but neither

has its two distinctive characters. Unfortunately, the minute size of the allotype male of *D. gracilis* made it impossible to determine enough characters to permit contrasts with other species.

Urocaridella gracilis has been reported as the host of two bopyrine (branchial) bopyrids in India (Chopra 1923), but neither it nor any other species of *Urocaridella* is previously known as a host of a hemiarthrine parasite.

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PERICLIMENES GONIOPORAE SP. NOV. (CRUSTACEA: DECAPODA: PALAEMONIDAE), A NEW COELENTERATE-ASSOCIATED SHRIMP

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ABSTRACT

A new species of *Periclimenes* (Crustacea: Decapoda: Palaemonidae), from the Indian Ocean and Great Barrier Reef, is recorded. *P. gonioporae* is primarily associated with scleractinian corals of the genus *Goniopora* and is closely related to *P. mahei* Bruce and *P. diversipes* Kemp. The name has appeared several times as a nomen nudum in the scientific literature since 1976 and is now validated. The distinguishing features of *P. gonioporae* are described, illustrated and discussed.

KEYWORDS: Crustacea: Decapoda: Palaemonidae, *Periclimenes gonioporae*, new species, nomen nudum validated, coral associate, Indo-West Pacific.

INTRODUCTION

In 1974, a description of a new shrimp was accepted for publication in a scientific journal. Despite several subsequent assurances that publication was imminent, the description remained unpublished. In the ensuing 15 years, the proposed name has unfortunately appeared in a number of other publications. The present communication will now regularize the use of the name and also provide some further relevant information on the same species. The reference numbers used in the 'material examined' section refer to the author's personal collection.

SYSTEMATICS

***Periclimenes gonioporae* sp. nov.**
(Figs 1-3, 4A)

Periclimenes diversipes - Bruce 1976a:11 (*non* Kemp 1922).

Periclimenes gonioporae - Bruce 1976b: 476 (nomen nudum), 1977:5 (nomen nudum), 1981:16, 17 (nomen nudum), 1983a:165 (nomen nudum), 1983b : 208 (nomen nudum).

Type material. The ovigerous female (#2157) is selected as holotype and deposited in the collection of the Northern Territory Museum, Darwin, NTM. Cr.006745, together with further paratype specimens (#2162, 2476). Paratypes are also deposited in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden, D37691, and the National Museum of Natural History, Washington, USNM 243226.

Additional examined. Kenya: (i) 1 male, 1 female, stn. 101, Ras Iwatine, Mombasa, 4°0.75'S 39°43.8'E, L.W.S., 13 January 1971, (#1354). (ii) 1 female, stn. 119, Ras Iwatine, Mombasa, 4°1.15'S 39°43.8'E, L.W.S., 26 July 1971, (#1535). (iii) 1 ovig. female, stn. 126, Shimoni, 4°39.25'S 39°03.5'E, L.W.S., 8 August 1971 (#1561). (iv) 1 male, 1 ovig. female, stn. 132, Ras Iwatine, Mombasa, 4°00.8'S 39°44.2'E, L.W.S., 3 October 1971 (#1601). (v) 1 ovig. female, stn. 180, Ras Iwatine, Mombasa, 4°01.15'S 39°43.78'E, L.W.S., 7 April 1974 (#2157). (vi) 5 male, 4 female, 1 ovig. female, stn. 180b, Ras Iwatine, Mombasa, 4°01.75'S 39°43.78'E, L.W.S., 11 April 1974 (#2162).

Australia : (vii) 1 ovig. female, Heron Island, Queensland, stn. DF-5, reef slope, 6.5m, 21 July 1976, coll. D. Fisk (#2423). (viii) 1 male, Heron Island, Queensland, L.W.S., coll. A.J. Bruce, (#2476). (ix) 1 ovig. female, Heron Island, Queensland, L.W.S., 30 March 1978, coll. D. Fisk (#2600).

Description. A small sized shrimp of about 1cm length, of slender, subcylindrical body

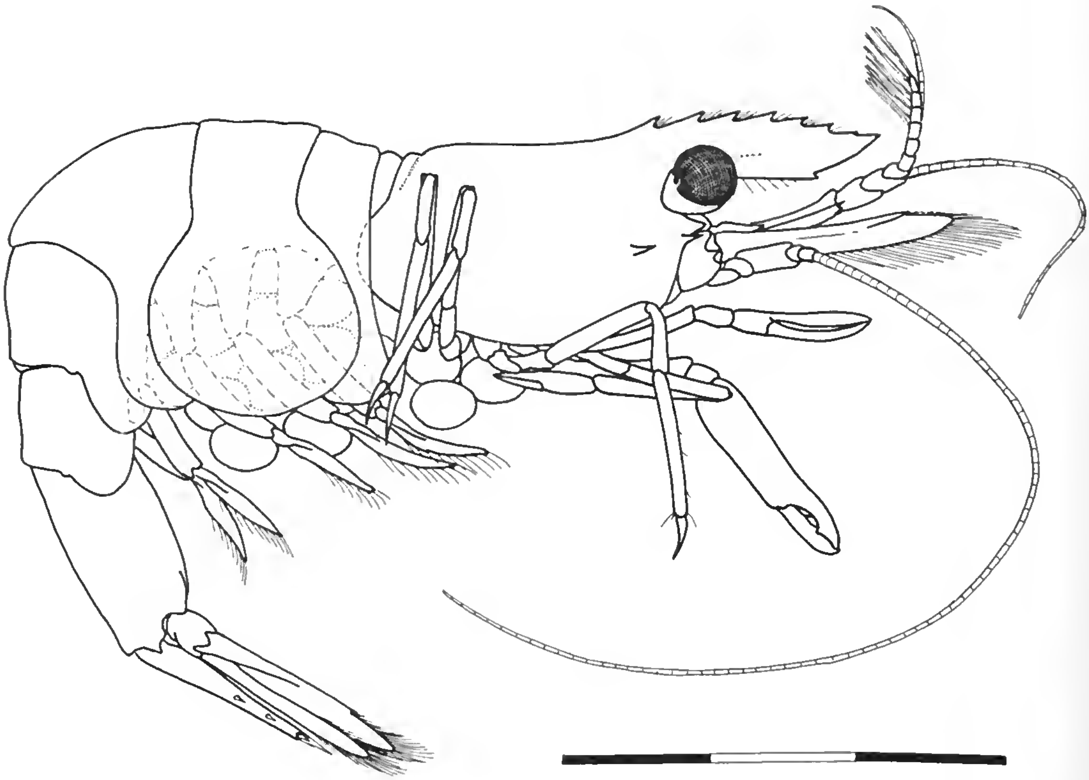

Fig. 1. *Periclimenes gonioporae* sp. nov., ovigerous female holotype, Ras Iwatine, Kenya. Scale bar in millimetres.

form, generally very similar in morphology to *Periclimenes diversipes* Kemp, 1922, so that a fully detailed description appears unnecessary. The following abbreviated description is based on Kenyan specimens.

Carapace smooth, with well developed rostrum, straight, horizontal, slightly exceeding intermediate segment of antennular peduncle, dorsal carina deep with dorsal margin straight or slightly convex, with 5-8 acute teeth, first generally situated slightly behind level of posterior orbital margin; ventral carina with proximal lower margin straight, setose, with single acute tooth at 0.75 of length, (very small or absent in some specimens), distal lower border convex, upcurved; orbit obsolete, inferior orbital angle acutely produced, antennal spine well developed, marginal, hepatic spine similar to antennal, on slightly lower level, anterolateral branchiostegite not produced, bluntly rounded.

Abdomen and caudal fan as in *P. diversipes*. Telson with two pairs of dorsal spines, small, at 0.5 and 0.75 of telson length; three pairs of posterior spines.

Eyes, antennae and mouthparts as in *P. diversipes*. Second maxilliped without podobranch. Third maxilliped with rudimentary arthrobranch, with single lamella only. First to third thoracic sternites moderately broad, fourth sternite broad, without slender median process, with low transverse ridge with small median notch, fifth to seventh sternites broadening posteriorly, unarmed.

First pereiopods slender, exceeding carpocerite by length of chela and carpus; chela with palm subcylindrical, slightly compressed, about 2.0 times longer than deep, fingers about 0.75 of palm length, slender, tapering, slightly compressed, with slightly laterally situated, entire cutting edges and small feebly hooked blunt tips; carpus about 1.5 times length of chela, gradually expanding distally, length about 6.5 times longer than distal width; merus subcylindrical, subequal to carpal length; ischium and basis as in *P. diversipes;* coxa with minute medial process.

Adult females with second pereiopods very unequal, dissimilar; major second pereiopod exceeds basicerite by carpus and chela; chela with palm subcylindrical, smooth, slightly compressed, about 3.4 times longer than wide; fingers equal to about 0.6 of palm length, dactylus 4.0 times longer than proximal depth,

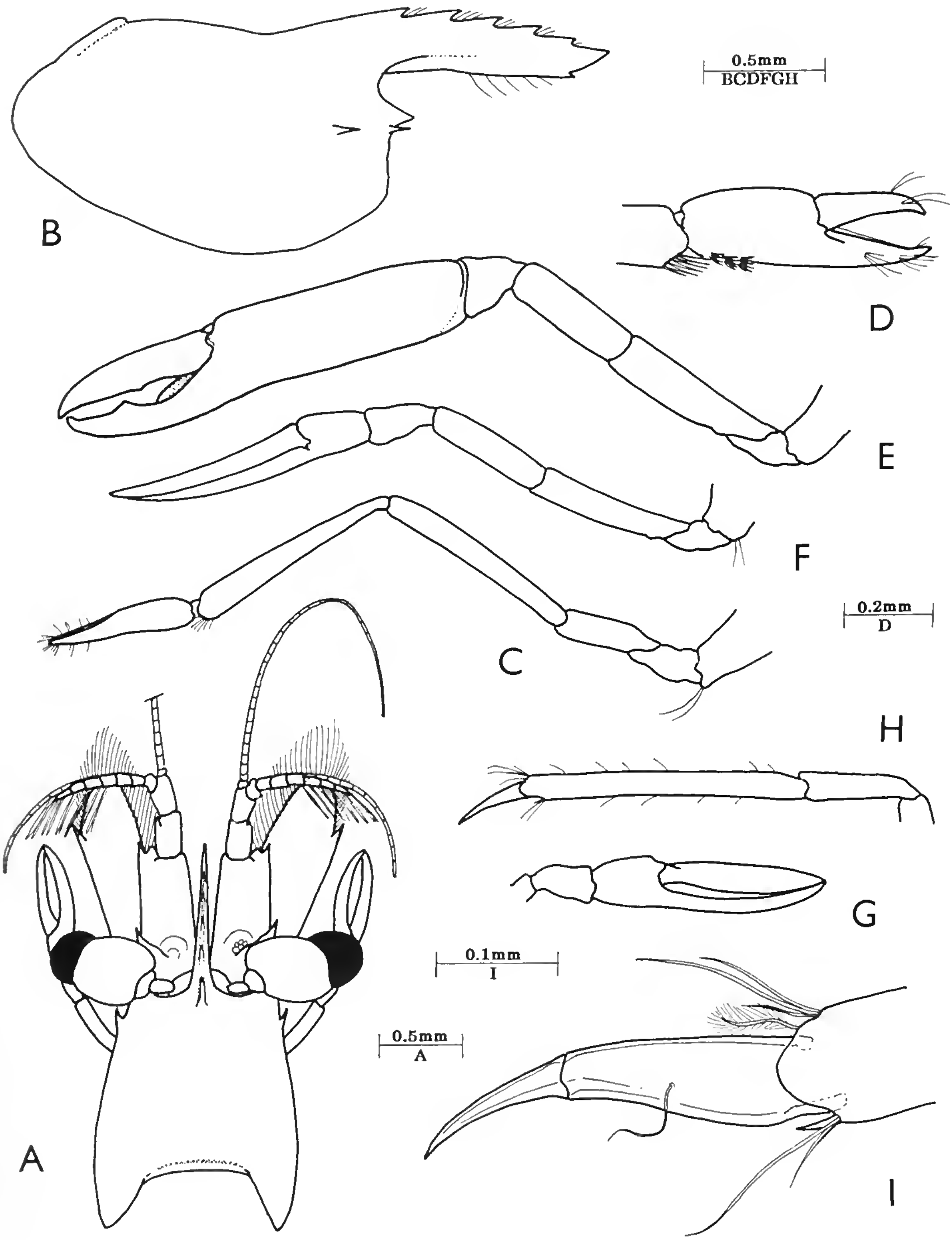

Fig. 2. *Periclimenes gonioporae* sp. nov., Ras Iwatine, Kenya. A, carapace, antennae, eyes, second pereiopods, dorsal aspect. B, carapace and rostrum, lateral. C, first pereiopod. D, same, chela. E, major second pereiopod. F, minor second pereiopod. G, same, chela. H, third pereiopod, dactyl, propod and carpus. I, same, dactyl and distal carpus. AB, male paratype. C-I, female holotype.

compressed, with small acute hooked tip, distal half of cutting edge straight, sharp, with feeble tooth proximally, proximal half sinuous, blunt; fixed finger curved, with small blunt tooth distally, central part of cutting edge with large deep U-shaped diastema, with large acute teeth distally, distal cutting edge sharp, straight; proximal to diastema, cutting edge shallowly grooved with elevated medial carina; carpus short, stout, about as long as distal width, about 0.25 of palm length, distally expanded, unarmed; merus subcylindrical, moderately compressed, 0.5 of palm length, 3.0 times longer than wide, feebly tapered proximally, unarmed; ischium about 1.3 times length of merus, 4.0 times longer than wide, feebly tapered proximally, unarmed; basis and coxa normal. Minor second pereiopod exceeds basicerite by chela and carpus; chela about 0.65 of major chela length, palm short, stout, about 0.25 of major chela palm length, 1.6 times longer than distal width, fingers 3.0 times longer than palm length, 1.3 times length of fingers of major chela, slightly bowed and scooped, cutting edges straight, entire, dactylus with small acute hooked tip distally, fixed finger with pair of small blunt protuberances distally; carpus, merus and ischium similar to major chela, more slender. Male second pereiopods subequal, similar, closely resembling minor second pereiopod of female, very short, reaching only to middle of intermediate segment of antennular peduncle.

Ambulatory pereiopods slender, third exceeding basicerite by dactyl, propod and carpus; dactyl slender, compressed, about 4.5 times longer than proximal width, unguis distinctly demarcated, about 0.6 of corpus length; propod about 3.3 times length of dactyl, 10.5 times longer than wide, uniform, with single small distoventral setiform spine only; corpus, merus, ischium, basis and coxa as in *P. diversipes*. Fourth pereiopod similar to third, fifth with single preterminal ventral spine on propod.

The Australian specimens show no significant differences from the Kenyan material. The single male specimen has the second pereiopods unequal, and very similar to the Kenyan females. Rostrum with only four acute dorsal teeth, with acute tip relatively longer, rostrum subequal to postorbital carapace length. Chela of major second pereiopod slightly longer than carapace length. Third pereiopod with dactylus about 0.36 of propod length, with very slender unguis, equal to about 0.76 of corpus length, corpus without evident setae. Male first pleopod with endopod about 0.5 of exopod length, distal 0.6 broadly expanded, with small acute lobe on medial margin distally, with five short simple spines on proximal third; distal and medial margins broadly rounded, non-setose. Second pleopod with endopod about 0.3 of exopod length, with appendices at 0.33 of medial margin; appendix masculina with corpus feebly tapering distally, about 4.7 times longer than proximal width, with two long terminal spines, about 0.8 of corpus length, with five spines of decreasing length proximally along the lateral margin.

Measurements (mm). Holotype female: postorbital carapace length, 1.9; carapace and rostrum, 3.45; total body length (approx.) 10.0; major chela 1.6; minor chela, 0.95; length of ovum, 0.5. Allotype male: postorbital carapace length, 1.2.

Colouration. Generally highly transparent. Ovigerous female with small groups of white chromatophores on ophthalmic somite, across sternites of seventh and eighth thoracic segments and, as broad transverse band, slightly swollen centrally, across centre of third abdominal somite; two small groups of white chromatophores present ventrally on second abdominal somite, with further small group on third sternite and pleura of third abdominal somite; minute red chromatophores scattered around bases of antennal peduncles, over ventral aspects of first to third abdominal segments and on peduncles of pleopods; gastric mill, hepatopancreas covered with white chromatophores; ovary translucent white, feebly speckled with red; cornea whitish; small group of white chromatophores present distally on carpus, merus and ischium of third to fifth pereiopods; first and second pereiopods, caudal fan transparent.

Host. The type specimens, and all others from Ras Iwatine, were found in association with scleractinian coral *Goniopora stutchburyi* Wells, and the specimens from Shimoni were associated with *Lobophyllia* sp. The Heron Island specimens were found in association with *Goniopora tenuidens* Milne-Edwards & Haime, *Galaxea fascicularis* (L.), *Porites cylindrica* Dana, and *Montipora* sp.

Habitat. Specimens were generally collected from protected lagoon sites at low water spring tide level to 0.5 m. The Heron Island

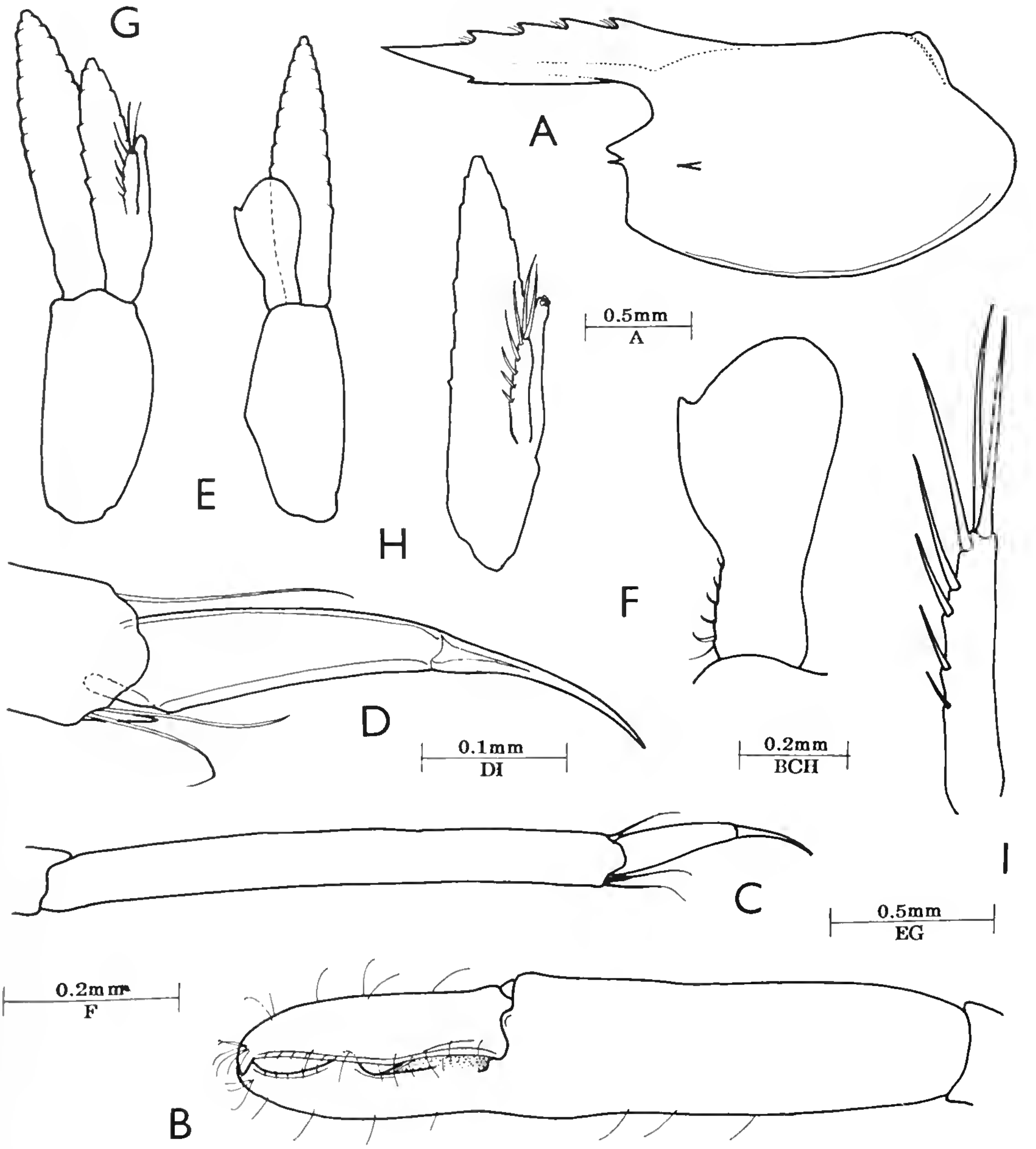

Fig. 3. *Periclimenes gonioporae* sp. nov., male paratype, CL 1.3 mm, Heron Island, Queensland. A, carapace and rostrum, lateral. B, chela of major second pereiopod. C, third pereiopod, propod and dactyl. D, same, dactyl and distal propod. E, first pleopod. F, same, endopod. G, second pleopod. H, same, endopod. I, same, appendix masculina.

specimen (# 2423) from *Montipora* was collected from 6.5m. Water temperature at the Kenyan sites was 28°C.

Associated fauna. The Kenyan specimens from *Lobophyllia* were associated with four small juvenile specimens of *Periclimenes brevicarpalis* (Schenkel).

Distribution. Type locality, Ras Iwatine, Mombasa, Kenya. Also known from Watamu and Shimoni, Kenya; La Réunion; Heron Island, Great Barrier Reef.

Systematic Position. *Periclimenes gonioporae* is a member of a small group of closely related coelenterate-associated species of the genus, consisting of *P. diversipes* Kemp, 1922, *P. jugalis* Holthuis, 1952, *P. mahei* Bruce, 1969, *P. madreporae* Bruce, 1969, *P. kempi* Bruce, 1969, *P. watamuae* Bruce, 1976

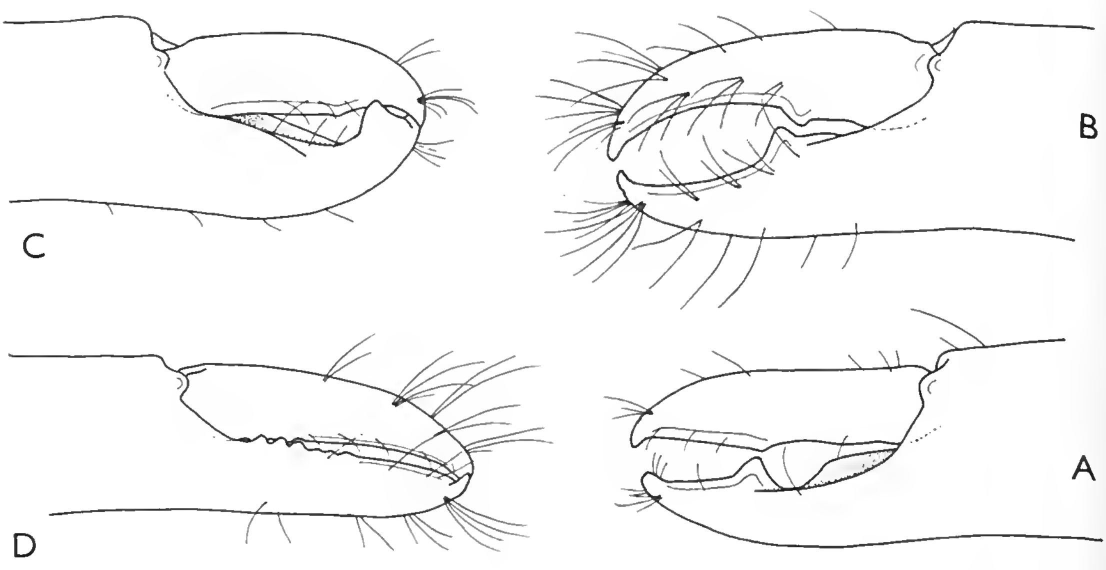

Fig. 4. Fingers of ovigerous females major second pereiopod. **A,** *Periclimenes gonioporae* sp. nov. **B,** *Periclimenes mahei* Bruce. **C,** *Periclimenes diversipes* Kemp. **D,** *Periclimenes madreporae* Bruce.

and *P. difficilis* Bruce, 1976a. Of these, *P. gonioporae* is most closely related to, and occupies a systematic position intermediate between *P. diversipes* and *P. mahei*.

The species of this group are most readily identified on the basis of the morphology of the chela of the major second pereiopod of ovigerous female specimens, the identification of isolated males with undeveloped major chelae and juveniles, except by association, is much more difficult and often not possible. In this respect, *P. gonioporae* shows a degree of chela modification that is constant and characteristic, based on the position and the degree of development of the tooth on the cutting edge of the fixed finger. *P. mahei* appears to represent the least specialized form of chela, with the fixed finger tooth at about the middle of the length of the cutting edge, with the sharp distal cutting edge distinctly concave. The dactylus has a well developed blunt tooth at about 0.4 of the cutting edge length, with the sharp distal cutting edge also concave, so that the closed fingers of the chela distinctly gape distally. The fixed finger is only very feebly cannulate proximally. *P. gonioporae* has a larger, more acute tooth at about 0.6 of the fixed finger length, with the sharp distal cutting edge straight, rather than concave, and the proximal cutting edge deeply cannulate, with a raised lateral carina, separated from the main tooth by a deep U-shaped diastema. The dactyl has only a small blunt tooth at about 0.5 of the length of its cutting edge, with the proximal edge being feebly sinuous, blunt, the distal edge straight, sharp. The closed fingers do not gape significantly. *P. diversipes* shows the most extreme modification. The tooth on the fixed finger is very large and acute, and occupies a position at about 0.8 of the length of the cutting edge, adjacent to the hooked tip of the finger, with the whole of the proximal cutting edge deeply emarginate and strongly cannulate, with a long low lateral carina. The dactyl has an obsolescent tooth at about 0.6 of the cutting edge length, with the short distal cutting edge sharp, slightly convex, the proximal cutting edge straight, blunt. The closed fingers gape slightly proximally to the tooth on the fixed finger. The minor second pereiopods in these species are essentially similar but differ slightly in proportions. In *P. gonioporae* the fingers are about 3.0 times the palm length and the carpus is subequal to the palm. In *P. diversipes*, the fingers are about 1.7 times the palm length and the carpus is about 1.5 times the palm length. In *P. mahei* the chela of the minor second pereiopod is subequal and similar to that of the major pereiopod (Bruce 1969, 1976b), with the fingers distinctly shorter than the palm.

The most simple means of distinguishing *P. gonioporae* from *P. diversipes* is by means of its characteristic pattern of white patches, which is quite lacking in *P. diversipes*, and which readily attracts the eye in the field. This

contrasts strongly with *P. diversipes*, which is mainly transparent, with inconspicuous fine red striae along the abdominal pleura. The colour pattern of *P. mahei* is as yet unknown.

DISCUSSION

The group of *Periclimenes* species to which *P. gonioporae* belongs are all of small size and with coelenterate associations and all, except *P. kempi*, which is found on alcyonarians, are commensals of scleractinian corals. *P. diversipes* has been found on the widest variety of hosts and is generally the commonest and most widely distributed species. It associates most characteristically with corals of the family Acroporidae, including *Acropora tenuis* and *A. variabilis*.

Periclimenes gonioporae, *P. kempi* and several related species appear to be from a natural group that is relatively easy to recognise but difficult to define precisely so as to exclude some other species of *Periclimenes* that do not appear to be closely related. Such a species is the distinctly larger *P. affinis* (Zehntner), a crinoid-associated shrimp, which appears closely related to others of similar habits, but, in contrast to them, has a simple dactyl on the ambulatory pereiopods, due probably to the loss of the usual accessory tooth found in the other species. *P. jugalis* Holthuis, 1952, is probably a member of this group, although it occurs in deeper water (13m) and it associates are unknown. Most of the species presently referred to this group occupy intertidal or shallow water habitats.

The *P. diversipes* group of species may be provisionally defined as small sized pontoniine shrimps, generally with well developed deep rostra with 4-9 dorsal teeth, 0-2 ventral teeth, without epigastric or supraorbital spines, orbit obsolete, inferior orbital angle produced, without inner flange, antennal and hepatic spines acute; third abdominal segment not posterodorsally produced; telson normal; antennae normal; eye with globular cornea, stalk without proximal articular lobe; ophthalmic segment without "bec ocellaire"; first pereiopods with simple fingers; second pereiopods generally unequal, most marked in adult females, subequal in some males, dissimilar or similar, chela smooth, carpus unarmed, merus without distoventral tooth; ambulatory pereiopods with dactyls short, simple, propods feebly spinulate; associated with coelenterates. The species may be distinguished by the following key.

Key for the identification of adult females of *Periclimenes diversipes* and related species

1. Fourth thoracic sternite unarmed..........2
   Fourth thoracic sternite with large linguiform median plate; R. 7/0...*P. difficilis* Bruce
2. Fingers of major second pereiopod dentate, non-spatulate..........................3
   Fingers of major second pereiopod non-dentate spatulate....................................7
3. Second pereiopods generally with chelae subequal, similar...................................4
   Second pereiopods generally with chelae unequal, dissimilar...............................5
4. Major second pereiopod with carpus about 0.6 of palm length; propods of ambulatory dactyls distoventrally distinctly spinulate; R.8/2.........................*P. jugalis* Holthuis
   Major second pereiopod with carpus less than 0.5 of palm length; ambulatory propods with small distoventral spinule only; R.6/1.....................*P. madreporae* Bruce
5. Fixed finger of major second pereiopod with tooth at less than 0.8 of length..........6
   Fixed finger of major second pereiopod with large acute tooth at about 0.8 of length, separated by deep notch from tip, dactylar tooth obsolete; R.5-7/0-2...*P. diversipes* Kemp
6. Major second pereiopod with fixed finger tooth large, acute, at about 0.6 of length, with large gap proximally; dactylar tooth obsolete, distal cutting edge more or less straight; R.5-7/0-1..*P. gonioporae* sp. nov.
   Major second pereiopod with fixed finger tooth at about 0.5 of length, blunt, with large gap proximally; dactylar tooth distinct, blunt, distal cutting edge concave; R.6-7/1..........................*P. mahei* Bruce
7. Major second pereiopod with fingers not exceeding palm length (0.3-0.6 times); R.6-8/1-2.......................*P. kempi* Bruce
   Major second pereiopod with fingers distinctly exceeding palm length (1.2-2.0 times); R.5/0-1.........*P. watamuae* Bruce

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ON A COLLECTION OF FISH AND PRAWNS FROM THE EAST ALLIGATOR ESTUARY, KAKADU NATIONAL PARK, AUSTRALIA

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ABSTRACT

52 species of fish and 16 species of prawns were collected from estuarine and inshore waters of the East Alligator River and Murgenella Creek in Kakadu National Park by beam trawl between September 1978 and May 1979. Sciaenids dominated the fish fauna, with *Johnius novaeguineae* being the most abundant species, followed by the gobioidid *Brachyamblyopus rubristriatus*, another sciaenid *Johnius weberi*, and the polynemid *Polynemus verekeri*. The prawns were dominated by a sergestid, *Acetes* sp., and a penaeid, *Atypopenaeus formosus*. Four species of fish are new records for Australia: *Ilisha megaloptera, Datniodes quadrifasciatus, Johnius macropterus* and *Johnius novaeguinae*. Four species do not appear to have been described: *Leiognathus* sp. 1; two sciaenids and a goby. The fish in this region are estuarine and inshore species typical of tropical Indo-Pacific waters with high turbidity and fluctuating salinities and, despite the restrictions of beam trawl sampling, include a number of species that occur in inshore waters of the Gulf of Carpentaria as well as tidal swamp areas near Darwin.

KEYWORDS: Estuaries, surveys, trawl, fish, crustacea, species distribution, tropical Australia

INTRODUCTION

The Ranger and Narbarlek uranium mines are located on tributaries of the East Alligator River system within the Kakadu National Park. The Alligator Rivers Region Research Institute was established under the Environmental Protection Act 1978 to conduct, coordinate and integrate research to ensure this region would, in future, be protected from any harmful effects of mining and processing of uranium ore (Anonymous 1985). Prior to this, various components of the environment and biota had been surveyed, including the fish communities of the upper freshwater habitats of the East Alligator River and Cooper Creek (Midgley 1974). However, no surveys had been made of the fish and crustacean fauna near the mouth or on the adjacent mudflats of the East Alligator River. A beam trawl survey of the fish and prawns was initiated by the CSIRO Division of Fisheries and conducted monthly from September 1978 to May 1979 as part of a larger study monitoring the reproductive cycle of barramundi, *Lates calcarifer* (Davis 1985). This paper presents information on the species collected by the beam trawl, and outlines some general patterns in their distribution and abundance prior to uranium mining in the region.

METHODS

Collections were made each month between September 1978 and May 1979 at seven stations near the mouth of the East Alligator River and along the mudflats of Murgenella and Saltwater Creeks to the north (Fig. 1) by using a roller beam trawl (described in Young 1975) towed from a dinghy, along the bottom against the direction of tidal flow. The specimens were washed and preserved in 5% v/v formaldehyde. Specimens were identified using keys or sent to specialists. Institutional abbreviations are as follows: CSIRO, CSIRO ISR Munro collection, Hobart; AMS, Australian Museum, Sydney.

RESULTS AND DISCUSSION

A total of 52 species of fish and 16 species of prawns were identified from 99 tows (Table 1). In addition to the gobies listed, there were

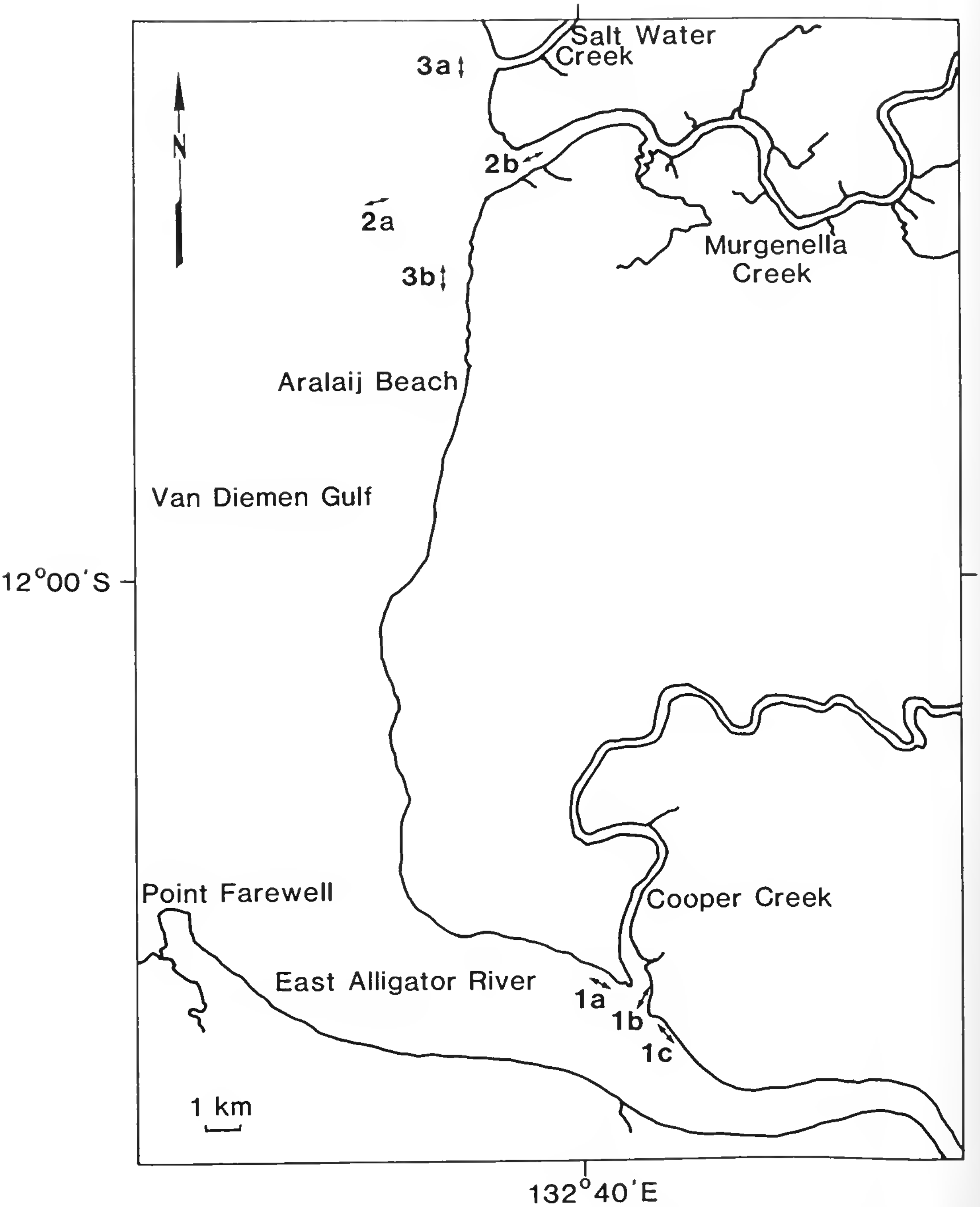

Fig. 1. Inshore and estuarine regions of East Alligator River and Murgenella Creek, Northern Territory, showing beam trawl stations and sites. Direction of tows indicated by arrows.

16 other species of gobies, mostly represented by single specimens, and being small juveniles could not be identified. Prawns dominated trawl samples, with *Acetes* sp. 1 and *Atypopenaeus formosus* being in particularly large numbers. The fish fauna was less abundant than the prawns but far more diverse. The sciaenid *Johnius novaeguinae*, was the dominant species followed by the gobioidid *Brachyamblyopus rubristriatus*, another sciaenid *Johnius weberi*, and the polynemid *Polynemus verekeri*.

All prawns identified to species have previously been recorded from the Northern Terri-

tory. Four species of fish are new records for Australia: *Ilisha megaloptera*, *Datniodes quadrifasciatus*, *Johnius macropterus* and *Gobiopsis macrostoma*. A further 6 species are new records for the Northern Territory: *Setipinna godvari*, *Cheroscorpaena tridactyla*, *Alepes melanoptera*, *Austronibia oedogenys*, *Otolithes ruber* and *Johnius novaeguinae*. Four species which do not appear to have been described have been deposited in the following institutions: *Leiognathus* sp. 1 (CSIRO B1988-1989); Sciaenid sp. 1 (CSIRO B1986) - considered to be an undescribed species of *Nibeini* close to *Daysciaena* (R. Mackay, personal communication), Sciaenid sp. 2 (CSIRO B1987) and Gobiid sp. 1 (AMS I. 22479.001-I.22482.001) - which is probably an undescribed genus (D. Hoese, personal communication).

All sciaenids, except two specimens of *Austronibea oedogenys*, were captured in the deeper water of the river channels (sites 1 and 2), rather than on the mudflats (site 3) and most were caught during January and Febru-

Table 1. List of prawn and fish species collected (by family and genus) together with length range (carapace length for prawns and standard length for fish, - denotes not measured) and abundance (rare<10; common, 10-100; abundant>100)

Taxon	Length range (mm)	Abundance
PRAWNS		
Penaeidae		
Atypopenaeus bicornis Racek and Dall, 1965	1-21	abundant
Atypopenaeus farmosus Dall, 1957	1-16	abundant
Metapenaeus eboracensis Dall, 1957	6-26	common
Metapenaeus ensis (de Haan, 1850)	16	rare
Metapenaeus demani (Roux, 1922)	9-23	common
Parapenaeopsis sculptilis (Heller, 1862)	3-29	abundant
Penaeus merguiensis de Man, 1888	13-108	rare
Sergestidae		
Acetes sp. 1	1-18	abundant
Lucifer sp. 1	1-2	abundant
Alpheidae		
Alpheus sp. 1	2-7	rare
Alpheus sp. 2	2-6	rare
Hippolytidae		
Hippolytid sp. 1	1-7	common
Hippolytid sp. 2	1-7	common
Palaemonidae		
Leander sp. 1	3-6	common
Macrobrachium sp. 1	5-20	rare
Palaemonid sp. 1	2-3	rare
FISH		
Clupeidae		
Escualosa thoracata (Valenciennes, 1847)	14-53	rare
Herklotsichthys sp. 1	55	rare
Ilisha megaloptera (Swainson, 1839)	25-55	rare
Engraulidae		
Papuengraulis micropinna Munro, 1964	15-94	common
Setipinna godvari Babu Rao, 1961	21-59	common
Stolephorus commersoni Lacepede, 1803	20-43	common
Stolephorus indicus van Hasselt, 1823	22-23	common
Thryssa hamiltoni (Gray, 1835)	48	rare
Thryssa kammalensis (Bleeker, 1849)	27-52	common
Thryssa setirostris (Broussonet, 1782)	25-28	rare
Harpadontidae		
Harpadon translucens Saville-Kent, 1889	44-102	rare
Ariidae		
Arius armiger De Vis, 1884	43-70	common
Arius berneyi (Whitley, 1941)	88	rare
Syngnathidae		
Hippichthys parvicarinatus Dawson, 1978	43	rare
Scorpaenidae		
Cheroscorpaena tridactyla Mees, 1964	6-51	common
Platycephalidae		
Platycephalid sp. 1	16-19	rare
Serranidae		
Serranid sp. 1	4	rare
Sillaginidae		
Sillago sp. 1	2	rare
Carangidae		
Alepes melanoptera Swainson, 1839	6-35	common
Leiognathidae		
Leiognathus sp. 1	7-20	common
Leiognathus equulus Forskal, 1775	8-12	rare
Lobotidae		
Datnoides quadrifasciatus (Sevastianov, 1809)	11-67	rare
Sciaenidae		
Austronibea oedogenys Trewavas, 1977	17-52	common
Johnius (Johnius) macropterus (Bleeker, 1835)	52	rare
Johnius (Johnius) weberi Hardenberg, 1936	9-57	abundant
Johnius (Johnieops) novaeguineae (Nichols, 1950)	5-99	abundant
Johnius (Johnieops) vogleri (Bleeker, 1853)	6-46	common
Nibea soldado (Lacepede, 1802)	8-52	common
Otolithes ruber (Schneider, 1801)	7-40	common
Sciaenid sp. 1	15-55	rare
Sciaenid sp. 2	38	rare
Scatophagidae		
Selenotoca multifasciata Richardson, 1844	5-6	rare
Mugilidae		
Mugilid sp. 1	11	rare
Polynemidae		
Polynemus sheridani (Macleay, 1884)	49	rare
Polynemus verekeri Saville-Kent, 1889	5-84	common
Callionymidae		
Callionymid sp. 1	4-7	rare
Gobiidae		
Apocryptodon sp. 1	18	rare
Boleophthalmus caeruleomaculatus McCulloch and Waite, 1917	10-15	rare
Drombus sp. 1	5-32	rare
Gobiopsis macrostoma Steindachner, 1861	10-60	rare
Gobiid sp. 1	20-30	rare
Oxuderces dentatus Eydoux and Souleyet, 1842	13-16	common
Periophthalmus sp.	9-10	rare
Scartelaos histophorus Cuvier and Valenciennes, 1837	12-14	common
Brachyamblyopus rubristriatus (Saville-Kent, 1889)	7-150	abundant
Taenioides jacksoni Smith, 1943	–	Rare
Eleotrididae		
Butis sp. 1	–	rare
Kurtidae		
Kurtus gulliveri Castlenau, 1878	6-32	common
Trichiuridae		
Trichiurus savala Cuvier, 1829	147	rare
Soleidae		
Pardachirus jaubertensis (Rendahl, 1921)	12-65	rare
Cynoglossidae		
Cynoglossus heterolepis Weber, 1910	119	rare
Cynoglossus maculipinnis (Rendahl, 1921)	33	rare
Paraplagusia guttata (Macleay, 1878)	8-45	rare
Tetraodontidae		
Tetraodontid sp. 1 (juveniles)	5-12	rare

ary. Sites 1 and 2 appear to be the nursery area for all the sciaenids and the preferred habitat for the adults of at least the smaller species that are likely to be caught by the beam trawl. Estuaries are important nursery grounds for the larvae and juveniles of many sciaenid species (Cowan and Birdsong 1985). Other species that were more abundant in the deeper water of the river channels than on the shallow mudflats were the prawns *Atypopenaeus bicornis* and *Parapenaeopsis sculptilus*, and the fish *Papuengraulis micropinna*, *Arius armiger*, *Cheroscorpaena tridactyla*, *Alepes melanoptera*, *Polynemus verekeri*, *Brachyamblyopus rubristriatus* and *Kurtus gulliveri*. *Stolephorus commersoni*, *Stolephorus indicus*, *Leiognathus* sp. 1 and *Oxuderces dentatus* were the only species clearly more abundant on the mudflats than in the river channels. *Lucifer* sp. 1 was present in very large numbers but only at sites 1 and 2 and it was absent at these sites in January and February, the months of lowest salinities. Other *Lucifer* species prefer salinities above $15^0/_{00}$ (Franks *et al.* 1972; Huff and Cobb 1979) and salinity probably limits the distribution of *Lucifer* in this study.

The fish fauna of the East Alligator estuary is rather different from that reported for other tropical estuarine areas in Australia. This can be attributed, in part, to the limited size range of fish able to be caught by beam trawl (Young and Wadley 1979). The fish fauna shows little affinity with that of the Dampier Region of North-west Australia (Blaber *et al.* 1985), sharing only 6 of the 165 species found in the latter region. Many of the species in that region occur in waters with low turbidity and constant salinity. The fish in our study area are estuarine and inshore species typical of tropical Indo-Pacific waters with high turbidity and fluctuating salinities. They show a closer affinity to the fish fauna in inshore waters of the Gulf of Carpentaria sharing 24% of the species caught by otter trawl (Rainer and Munro 1982) and the fauna of tidal swamp areas near Darwin (Davis 1988) where 20% of the species caught in tidal traps were also caught in the East Alligator estuary.

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A NOTE ON THE STATUS OF *GEHYRA BALIOLA* (DUMÉRIL AND DUMÉRIL, 1851) IN AUSTRALIA.

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ABSTRACT

An examination of specimens of *Gehyra* Gray from Papua New Guinea, the Torres Strait Islands, and Cape York Peninsula reveals that *Gehyra baliola* is predominantly a New Guinean species. Specimens collected from the Australian mainland which have in the past been attributed to *G. baliola* are not from this taxon. The only specimens of *G. baliola* found in Australian Territory occur on Darnley and Murray Islands in the northern Torres Strait. *Gehyra dubia* is present on several of the more southerly Torres Strait islands, whereas *G. oceanica* is not present in this area.

KEYWORDS: Reptilia, Gekkonidae, *Gehyra baliola*, distribution.

INTRODUCTION

The gekkonid lizard genus *Gehyra* has been the subject of considerable taxonomic revision. A number of new taxa have been described and the species composition for Australia now stands at 16: *G. australis* Gray, *G. baliola* (Duméril and Duméril), *G. borroloola* King, *G. catenata* Low, *G. dubia* Macleay, *G. minuta* King, *G. montium* Storr, G. *nana* Storr, *G. occidentalis* King, *G. pamela* King, *G. pilbara* Mitchell, *G. punctata* (Fry), *G. purpurascens* Storr, *G. robusta* King, *G. variegata* (Duméril and Bibron), *G. xenopus* Storr. The distribution and taxonomic status of several *Gehyra* species in northern Australia, particularly those on Cape York Peninsula and the Torres Strait Islands is uncertain. King (1983, 1984a) in reviewing the systematics of the previously considered widespread *G. australis*, recognised it as comprising 5 taxa: *G. australis*, *G. borroloola*, *G. robusta*, *G. occidentalis* and *G. dubia*. The latter species was restricted to Australia, east of the Gulf of Carpentaria and north along Cape York Peninsula including some Torres Strait Islands. From Cape York, Cogger (1986) listed *G. dubia*, *G. nana*, and possibly *G. baliola* ("status uncertain") suggesting that *G. baliola* was to be found as far south as Weipa on the Cape York Peninsula. From the Torres Strait Islands, Cogger (1986) included *G. baliola* and *G. oceanica*, but not *G. dubia*.

This communication clarifies the status of *G. baliola* on the Torres Strait Islands, and comments on the occurrence of *G. dubia* and *G. oceanica* in this region. The specimens examined came from the following institutions: AM, Australian Museum, Sydney; PNGM, National Museum and Art Gallery of Papua New Guinea; MNHN, Muséum National d'Histoire Naturelle, Paris.

SYSTEMATICS

Gehyra baliola (Duméril and Duméril)

Hemidactylus baliolus Duméril and Duméril, 1851: 38.
Peripia marmorata Macleay, 1877: 99.
Peripia brevicaudis Macleay, 1877: 99.

Type material: HOLOTYPE - MNHN 6574, New Guinea. HOLOTYPE of *Peripia marmorata*, AM R.29943, (MM MR 1201) Katau, near the Binaturi River, New Guinea. LECTOTYPE of *Peripia brevicaudis*, AM R.29947 (MM MR 931). Darnley Island, Torres Strait, Qld.

Additional Material. PAPUA NEW GUINEA: AM R.12156-57, 30 miles above D'Albertis Junction, Fly River, 6°00'S 141°15'E; AM R.24280, Lake Murray, 6°48'S

A
B
C

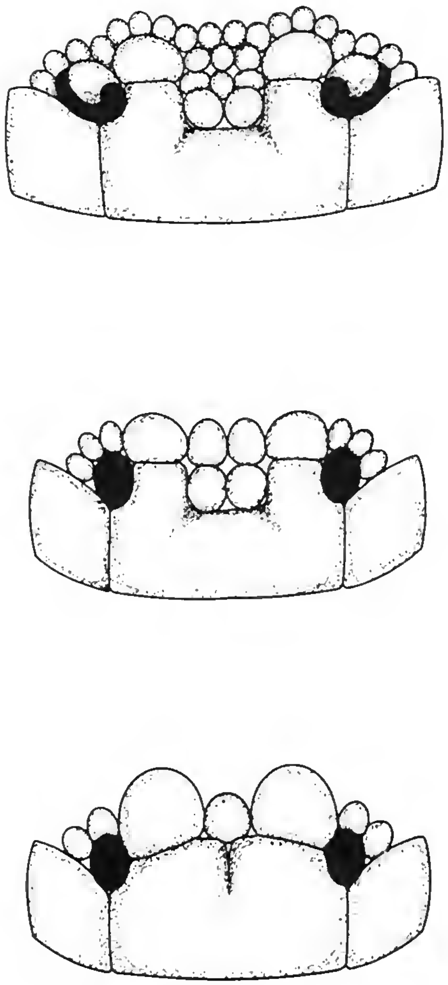

Fig. 1. A, A diagrammatic representation of the snout tip of a typical *Gehyra baliola* drawn from AM R.29947 from Darnley Island, which was also the lectotype of *Peripia brevicaudis* Macleay, 1877. **B**, A diagrammatic representation of the tip of the snout of a *Gehyra* sp. AM R.48368 from Saibai Island, Torres Strait. Note the difference in form of the 'U' shaped rostral and associated nasal and internasals in this and *Gehyra baliola*. **C**, A diagrammatic representation of the tip of the snout of *Gehyra* sp. AM R.48220 from Saibai Island, Torres Strait. This morphology is characteristic of *Gehyra dubia*.

141°26'E; AM R.122116, Wipim, 8°47'S 142°53'E; AM R.122399-402, Fogamaiyu, 6°31'S 143°05'E; AM R.122403-06, Waro Bush Camp, 6°31'S 143°11'E; PNGM 23654, Brown River, 9°20'S 147°30'E; QUEENSLAND: AM R.43899-900, AM R.44228-29, AM R.45912-13, AM R.45944, AM R.46090, Murray Island, Torres Strait, 9°56'S 144°04'E.

Comparative specimens of *Gehyra* spp from Torres Strait and Cape York Peninsula examined: AM R.42252-53, Hammond Island, 10°32'S 142°13'E; AM R.48220-21, AM R.48223, AM R.48237, AM R.48306, AM R.48331, AM R.48345, AM R.48368, AM R.48371, Sabai Island, 9°24'S 142°42'E; AM R.48396-98, AM R.48418, Horn Island, 10°37'S 142°17'E; AM R. 64233, Moa Island, 10°11'S 142°16'E; AM R.82377, AM R.82434, AM R.91618, Weipa, 12°38'S 141°52'E; AM R.91455, AM R.91637, 67km N. Weipa, 12°03'S 141°53'E; AM R.94160-62, Portland Roads, 12°36'S 143°25'E; AM R.94350-51, Cockatoo Creek, 11°40'S 142°21'E; AM R.94405-06, 53km E. Weipa, 12°45'S 142°16'E; AM R.94471, Iron Range, 12°46'S 143°16'E; AM R.94517, Tozer Range, 12°47'S 143°13'E.

The distribution of *Gehyra baliola* in Australia. In 1963 Kluge reclassified a series of specimens from the Macleay Museum collection, placing these into what he considered to be a more appropriate nomenclature. Among the changes made was incorporating *Peripia marmorata* Macleay (collected at Katau, New Guinea) into synonymy with *Gehyra baliola* (Duméril and Duméril, 1851), a common New Guinean form, and the inclusion of *Peripia brevicaudis* Macleay (collected on Darnley Island, Torres Strait, Queensland) with *Gehyra baliola*. Thus, *Gehyra baliola* became an Australian species. However, the diagnostic characteristics provided for *G. baliola* by Kluge (1963) have a series of deficiencies preventing clear species identification.

Table 1. Morphometric and meristic characteristics from 25 specimens of *Gehyra baliola* sampled from localities shown in Fig. 2. Measurements are in mm.

CHARACTERISTIC	MEAN	RANGE
Snout-vent length	84.4	67.0 - 101.0
Tail length (n = 5)	72.8	67.0 - 79.0
Forelimb length	23.0	19.1 - 30.6
Hindlimb length	29.1	22.4 - 36.0
Head width	14.4	12.1 - 17.9
Head depth	8.8	7.0 - 10.8
Ear-snout length	19.0	16.2 - 23.1
Nostril-snout length	1.5	1.1 - 2.0
Eye-snout length	8.6	7.2 - 10.9
Postmental scale length	2.6	2.2 - 3.1
Number of scales between eyes	44.7	36.0 - 50.0
Number of granular internasal scales	9.0	6.0 - 12.0
Number of supralabial scales	12.6	11.0 - 14.0
Number of infralabial scales	10.4	9.0 - 12.0
Number of mid-body scale rows	143.8	128.0 - 162.0
Number of fourth toe, subdigital lamellae	14.7	12.0 - 16.0
Number of preanal pores	31.8	28.0 - 34.0
Number of postanal spines	3.13	3.0 - 4.0
Tail length to snout-vent length ratio (n=5)	1:1.2	1:1.1 - 1:1.3
Head depth to head width ratio	1:1.6	1:1.5 - 1:2
Head depth to head length ratio	1:2.2	1:1.8 - 1:2.5
Postmental scale length to snout-vent length ratio	1:32.7	1:28.3 - 1:42.7

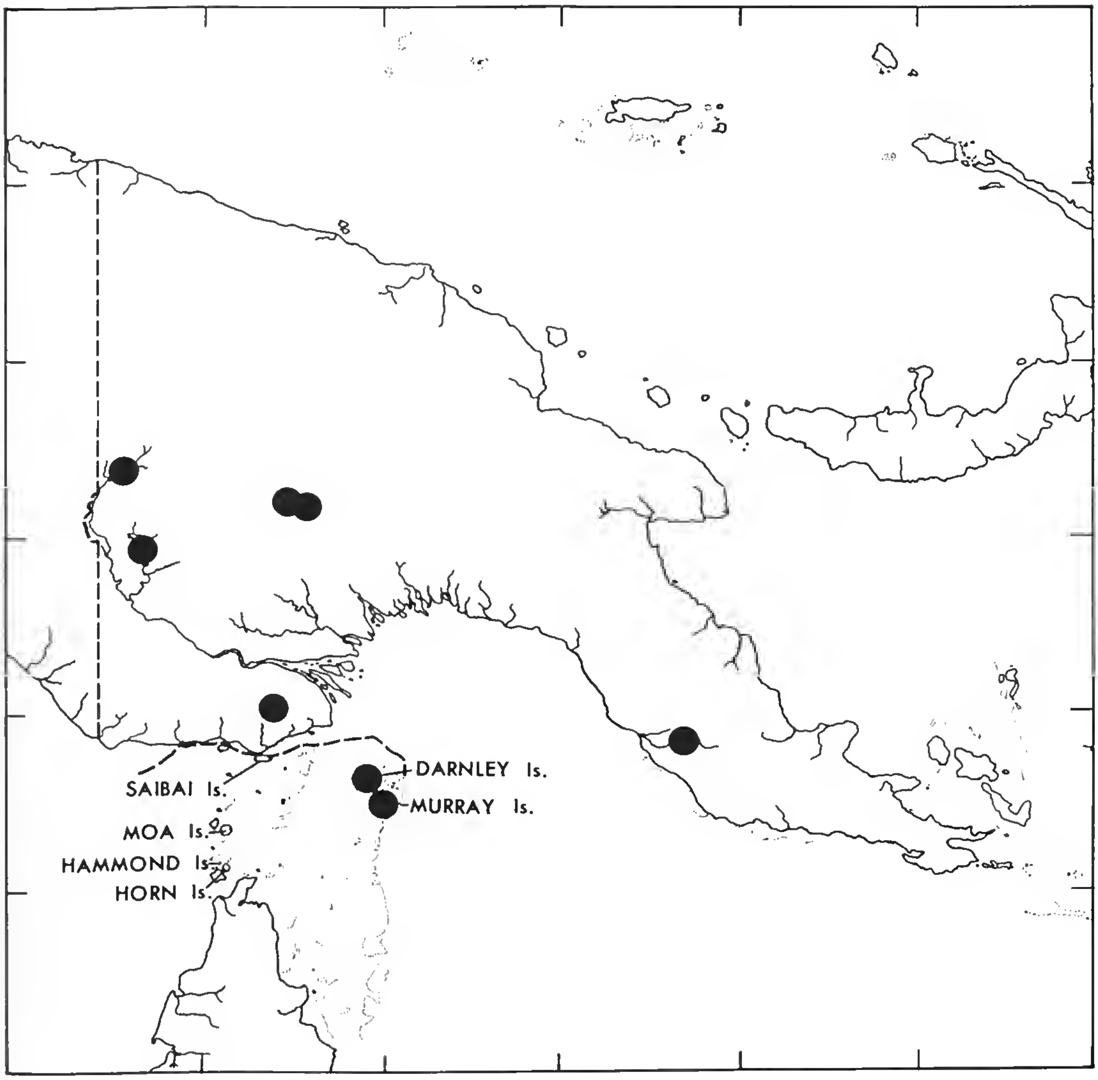

Fig. 2. The distribution of specimens of *Gehyra baliola* examined in this study.

The diagnostic feature used by Cogger (1986) to differentiate *G. baliola* from *G. dubia* is the presence of a cutaneous fold along the hind edge of the hindlimb. Similarly, King (1983) also defined this character as the main distinguishing feature between *G. baliola* and the Australian *G. australis* species group members. Because of the difficulty of distinguishing specimens of *G. baliola* on this feature alone, a detailed morphological analysis has been made on *G. baliola* to redefine its dominant characteristics.

Morphology. A series of 25 specimens of *Gehyra baliola* from New Guinea and certain Torres Strait Islands were examined and a detailed tabular summary of the morphological characteristics of this species is provided in Table 1.

Gehyra baliola is a distinctive species readily distinguished by the following combination of characters: large size (maximum SVL 101mm); number of preanal pores in males 28-34; presence of a cutaneous fold along hind edge of hindlimb (best developed in adult males); toes strongly dilated with 12-16 subdigital lamellae beneath expanded portion of fourth toe, the distal lamellae are divided by a median groove; internasal region fragmented, the "U" shaped rostral scale with 6-12 small granular scales filling the gap to the top of the adjacent large internasals (Fig. 1); the nasal aperture typically "comma" shaped with the

nasal scale occluding part of the aperture (Fig. 1); tail ovoid, dorso-ventrally compressed with pronounced lateral ridges giving impression of being roughly triangular in section. This combination of characters serves to separate *G. baliola* from all other Australian *Gehyra*.

Of the abovementioned morphological characteristics, the rostral scale "shape" appears to be the least robust, for whilst a "U" shaped rostral is characteristically present in *Gehyra baliola* specimens, a similarly shaped rostral is present in odd specimens from the *G. australis* complex (Fig. 1). Kluge (1963) assigned R 29947, a lectotype of *Peripia brevicaudis*, to *Gehyra baliola* using this among other characters, yet R 29949 which he synonymised with *G. variegata* also has a "U" shaped rostral. It is preferable to use the suite of characters outlined above rather than any single character.

Examination of the holotype of *Hemidactylus baliolus* (MNHN 6574) (the holotype of *Gehyra baliola*), the holotype of *Peripia marmorata* (R 29943), and the lectotype of *Peripia brevicaudis* (R 29947) leaves little doubt that all three are *Gehyra baliola*, confirming the distribution of this species in Australia. Examination of all specimens of Torres Strait *Gehyra* in the Australian Museum show that *G. baliola* occurs only on the volcanic Murray and Darnley Islands on the northeastern edge of the Great Barrier Reef, and on mainland New Guinea. The distribution of specimens of *Gehyra baliola* examined in this study is shown in Figure 2. The specimens of *Gehyra* referred to by Cogger (1986) as *G. baliola* from the northern portion of Cape York Peninsula presumably belong to an undescribed taxon. Indeed King (1984b) has shown that these specimens are chromosomally distinct from *G. dubia*.

The status of *Gehyra dubia* and *Gehyra oceanica* in Torres Strait. Specimens of *Gehyra* inhabiting the northern Torres Strait Islands differ from mainland and southern Torres Strait Island specimens in being of larger size, and in having a tendency for the skin to be shed in large patches during capture. This northern form was observed (by Sadlier) on Yam Island where it was abundant, and active at night both on tree trunks and low outcropping boulders. A detailed morphological examination of these specimens is necessary before the status of this form is determined. It appears that *G. dubia* is also present on some of the more southern islands in Torres Strait: i.e. Horn, Hammond and Moa Islands (Fig. 2).

Cogger (1986) records *Gehyra oceanica* questioningly from the tip of Cape York and with certainty from some Torres Strait Islands. Mitchell (1965) also questions previous citations of this species from mainland Australia, but comments on the existence of an old exhibition in the South Australian Museum labelled *Gehyra mutilata* from Mulgrave Island, which Mitchell assumed to be a specimen of *G. oceanica* from the Torres Strait. There is little chance of confusing *G. oceanica* with other Torres Strait *Gehyra* species. *Gehyra oceanica* has numerous undivided lamellae beneath the expanded portion of the toes; a rounded tail (in section) with paired enlarged subcaudal scales; generally a single internasal scale; and numerous (26-44) preanal pores. The first 3 of these characters will distinguish *G. oceanica* from *G. baliola*, and the latter 2 from *G. dubia*. We have been unable to locate specimens of this species in Australian museum collections from either mainland Australia or the Torres Strait Islands, and its presence in these regions remains unsubstantiated aside from the reference by Mitchell to the exhibition specimen from Mulgrave Island. We therefore believe that *Gehyra oceanica* does not occur on these islands and that large specimens of *G. baliola* may have been confused with that species.

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KARYOTYPIC EVOLUTION IN*GEHYRA* (GEKKONIDAE: REPTILIA). V. A NEW SPECIES FROM PAPUA NEW GUINEA AND THE DISTRIBUTION AND MORPHOMETRICS OF *GEHYRA OCEANICA* (LESSON)

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ABSTRACT

A new species of *Gehyra* Gray from Papua New Guinea is described. Previously confused with *G. oceanica* and *G. vorax*, this species is distinguished from these and other congeners by morphological characters and karyotype morphology. The widely distributed *G. oceanica* is surveyed morphologically and chromosomally, and the island populations of this species which were analysed appear to be conspecific.

KEYWORDS: Reptilia, Gekkonidae, *Gehyra*, new species, *oceanica*, New Guinea, karyotype.

INTRODUCTION

Chromosomal analysis at the population level has been successfully used to determine the independent gene pools present in morphologically heterogeneous and taxonomically unstable gekkonid species (King 1979, 1982a, 1983a, 1984a). Once this step has been taken it is possible to analyse the morphology of specimens taken from the distributions of these chromosome races with the view to a taxonomic revision. Such an approach has been used with gekkos from the *Gehyra australis* Gray species complex (see King 1982a, 1983a, 1983b, 1984b), and led to a redefinition of *G. australis*, the resurrection of *G. dubia* Macleay, and the description of *G. pamela* King, *G. borroloola* King, *G. robusta* King, and *G. occidentalis* King. Each of these species is morphologically and chromosomally distinct. The same approach has been used successfully in other *Gehyra* by King (1979, 1982b), in the genus *Phyllodactylus* by King and Rofe (1976), King and King (1977), Storr (1987), and in *Diplodactylus* by King (1977), and Storr (1979).

The present paper describes a new species, which was reported earlier as being chromosomally distinguishable from other *Gehyra* (King 1984a). In addition, a report on a chromosomal survey of the widely distributed species *G. oceanica* (Lesson) is made. This paper further investigates the evolution of *Gehyra* in general.

MATERIALS AND METHODS

Chromosomal Analysis. A series of 18 specimens of *G. oceanica* collected throughout the Pacific basin were examined chromosomally. The localities for these animals are shown in Table 1.

Table 1. The localities and sex of specimens of *Gehyra oceanica* which were analysed chromosomally.

Locality	Number of specimens male	immature	female
Marquesas Islands	1	–	3
Tahiti	2	1	2
Austral Islands	–	–	1
Moorea	–	–	1
Koro Island, Fiji	1	–	–
Tarawa Island, Kirabati	–	–	1
Upolu Island, West Samoa	1	–	1
Yanduataba Island, Fiji	1	–	1
Rarotonga Island, Cook Islands	–	1	–
	6	2	10

Chromosomal analyses were made on colchicine arrested air dried intestinal epithelial cells obtained by the technique defined by

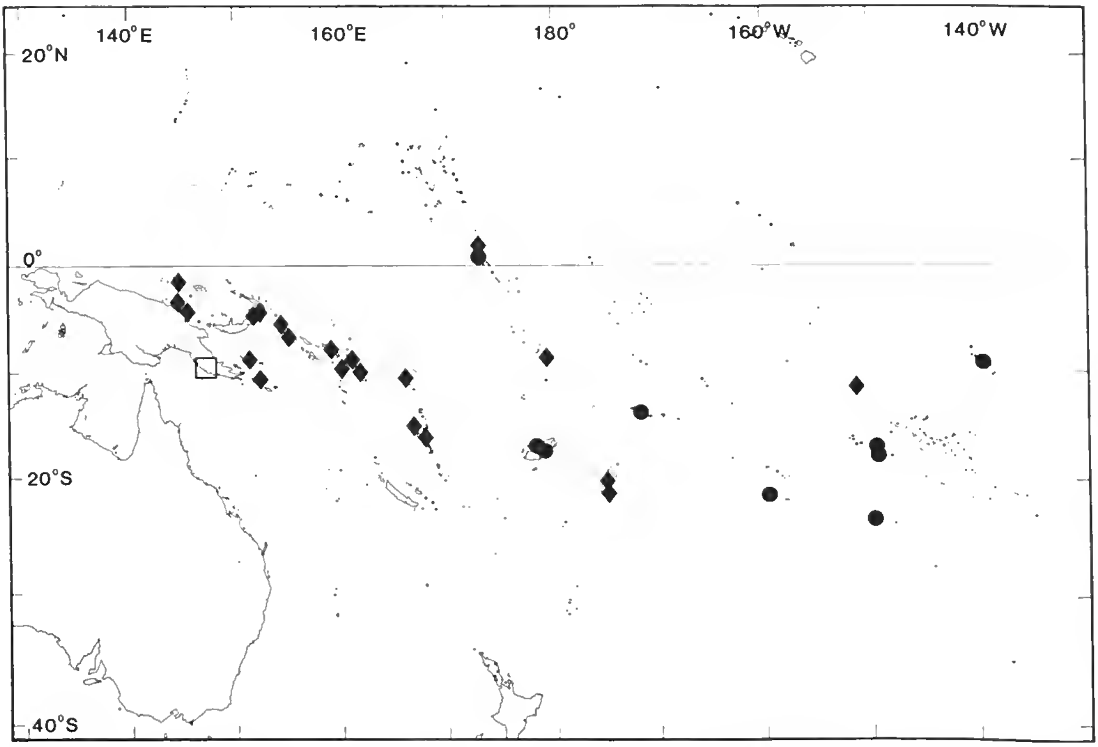


Fig. 1. A map of the Pacific Basin showing the distribution of *Gehyra oceanica* analysed in this study. Closed circles represent specimens karyotyped, closed diamonds represent specimens analysed morphologically. The known distribution of *Gehyra membranacruralis* is included in the open square.

King and Rofe (1976). In addition, short term leucocyte cultures were made on certain specimens using the technique described by King and King (1975).

Morphological analysis. A detailed morphometric and meristic analysis was made on a series of 90 specimens of *G. oceanica*, and 7 specimens of an undescribed species found in Papua New Guinea. Eighteen measurements were made on each specimen using micrometer adjusted callipers and/or steel rule.

Of the measurements taken, the following require individual definition:

1. Ear-snout length: measured from the anterior margin of the ear opening to the tip of the snout.
2. Nostril-snout length: measured from the anterior margin of the nostril opening to the tip of the snout.
3. Eye-snout length: measured from the anterior margin of the eye to the tip of the snout.
4. Number of scales between eyes: measured in a straight line between the dorsal margins of the eyes.
5. Number of fourth toe subdigital lamellae: only those lamellae under the expanded portion of the fourth toe were counted.

A series of additional species of *Gehyra* were also examined for comparison. These include the holotypes of *G. marginata* Boulenger (BMNH 87.1.20.1) and *G. baliola* (Duméril and Duméril) (MNHN 6574), specimens of *G. vorax* Girard, and members of the *G. australis* species complex (*sensu* King 1983).

The following abbreviations are used in the text: AM, Australian Museum; NTM, Northern Territory Museum of Arts and Sciences; PNGM, National Museum and Art Gallery of Papua New Guinea; BMNH, British Museum of Natural History; MNHN, Muséum National d'Histoire Naturelle, Paris.

SYSTEMATICS

Genus *Gehyra* Gray

Gehyra Gray, 1834:100 (type species *Gehyra pacifica* Gray, 1834, by monotypy). (see Cogger *et al* 1983:86-87 for synonymy).

Diagnosis. (modified after de Rooij 1915) Limbs pentadactylic; digits strongly dilated, free or webbed at the base; inferior transverse lamellae undivided, grooved or medially divided; distal phalanges free, elongate, compressed, clawed, rising from within the extremity of the dilated part; inner digits without free distal phalange, clawless, or with a very indistinct retractile claw; dorsal surface covered with small juxtaposed scales; ventral surface with cycloid imbricate scales; pupil vertical; males with femoral or preanal pores.

Distribution. Madagascar; Asia; Indo-Malayan Archipelago; Australia; New Guinea and Pacific Islands.

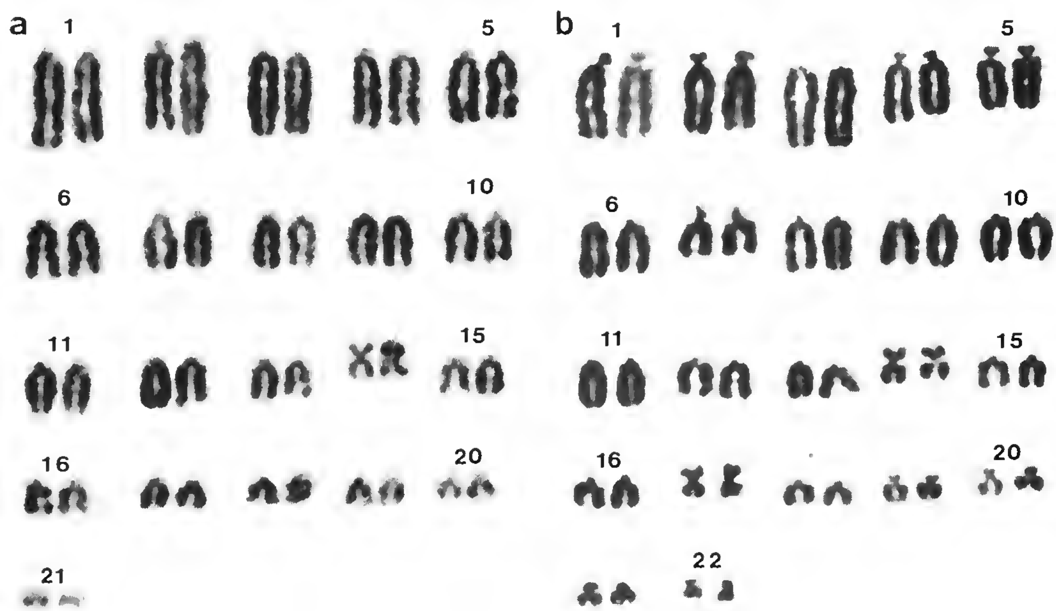
Remarks. Of the many species of *Gehyra* attributed to Papua New Guinea by de Rooij (1915) and Whitaker *et. al.* (1982), we have been able to redefine the list to the following: *Gehyra baliola* (Duméril and Duméril), *G. interstitialis* Oudemans, *G. papuana* Meyer, *G. leopoldi* Brongersma, *G. mutilata* (Wiegmann), *G. oceania* (Lesson) and *G. variegata* (Duméril and Bibron).

A number of other species of *Gehyra* have been synonymized. Thus, Kluge (1963) synonymized *Peripia papuensis* Macleay, with *Hemidactylus frenatus* Duméril and Bibron. Similarly, Wermuth (1965) synonymized *G. lampei* Andersson with *G. papuana* Meyer and *G. beebei* Annandale with *G. mutilata* (Wiegmann). The status of *Gehyra variegata* in Papua New Guinea remains uncertain and is currently under investigation.

Of these species, *G. oceanica* is found throughout the islands of Polynesia and Melanesia in the Pacific Basin. There is now doubt, however, as to whether this species does actually occur on mainland Papua New Guinea or West Irian. Although de Rooij (1915) and Whitaker *et. al.* (1982) recorded *G. oceanica* from that island, there has been a considerable amount of confusion among herpetologists who have referred specimens of *G. baliola* and an undescribed species of *Gehyra* (which is morphologically similar to both *G. oceanica* and *G. vorax*), to *G. oceanica*.

The second species questionably referred to the fauna of Papua New Guinea is *G. vorax* Girard. This species is known from Fiji, Vanuatu (New Hebrides) and the Loyalty Islands. De Rooij (1915) and Whitaker *et. al.* (1982) suggest that *G. vorax* is also found in Papua New Guinea. However, specimens from this island are morphologically distinct from *G. vorax*, and these appear to be from the same undescribed species which has been confused with *G. oceanica*.

Fig. 2. a, The mitotic chromosomes of *Gehyra oceanica* female collected from Tahiti. Note 2n=42 karyotype and pair 14 metacentric elements characteristic of most *Gehyra*. **b**, The mitotic chromosomes of *Gehyra membranacruralis* male collected from Port Moresby, Papua New Guinea. Note the characteristic 2n=44 karyotype with metacentric pairs 14 and 17.



Gehyra oceanica (Lesson)
(Figs 3, 6)

Gecko oceanicus Lesson, 1830: 42, pl. 2 fig. 3 (see Cogger *et. al.* 1983:88-89 for synonymy).

Type material. Syntypes: MNHN 1776, 6608 Ovalan Island = Kusai, Caroline archipelago 08°00'N 14°00'E; MNHN 2293, Tongatabu Tonga, 20°00'S 175°00'W.

Comparative material of *Gehyra oceanica*. PAPUA NEW GUINEA - AM R.0276, Duke of York Island, Bismarck Archipelago, 04°S 10'E 152°28'E; AM R.4561, Maron Island, Bismarck Archipelago, 01°30'S 145°00'E; AM R.18801-02, Buin, Bougainville Island, 06°52'S 155°42'E; AM R.24745-49, AM R.24770-71, AM R.24965, AM R.25042-43, AM R.25177, AM R.28768-69, AM R.28900, Karkar Island, 04°40'S 146°00'E; AM R.29832, Manam Island, 04°04'S 145°04'E; AM R.102942, Kuia Island, Trobriand Islands, 08°35'S 150°52'E: AM R.111237-38, Melilup, Bougainville Island, 05°49'S 154°32'E; AM R.111239, Ramazon River, Bougainville Island, 05°42'S 154°56'E; AM R.111240, Rabaul, New Britain Island, 04°11'S 152°11'E; AM R.111241, Buka Island, 05°15'S 154°38'E; AM R.111242-45, Kunua, Bougainville Island, 06°00'S 155°00'E; AM R.124813, Kiriwina Island, Trobriand Islands, 08°25'S 151°05'E; AM R.124950-53, AM R.125007, Misima Island, Louisade Archipelago, 10°42'S 152°50'E; PNGM 23152, Takani, Bougainville Island, 06°00'S 155°00'E.

PACIFIC OCEAN - AM R.0305-10, AM R.1801, New Hebrides, 15°00'S 168°00'E; AM R.2075-78, AM R.2293, Funafuti Atoll, Ellice Islands, 08°30'S 179°12'E; AM R. 3898, Flint Island, Line Islands, 11°25'S 151°48'W; AM R.4770, Samoa, 14°00'S 172°00'W; AM R.7209-10, Tonga Islands, 20°00'S 175°00'W; AM R.7246, Solomon Islands, 08°00'S 159.00'E; AM R.8799 Ysabel Island, Solomon Islands, 08°03'S 159°02'E; AM R.69571, Olu Malau Islands, Solomon Islands, 10°10'S 161°57'E; AM R.87400-05, Britaama, Malaita Island, Solomon Islands, 08°24'S 160°36'E: AM R.91009, Marau, Guadalcanal Island, Solomon Islands, 09°26'S 160°25'E; AM R.91052-56, Boromole, Nggela Sule, Solomon Islands, 09°03'S 160°18'E; AM R.9029-30, Trevanian Island, Santa Cruz Islands, 11°00'S 166°15'E; AM R.9042, Vanikoro Island, Santa Cruz Islands, 11°42'S 166°50'E; AM R.11391, Santo Island, New Hebrides, 15°30'S 166°40'E; AM R.31256, Upolu Island, West Samoa, 13°55'S 171°45'W; AM R.96555-57, AM R.96581-83, Eua Island, Tongatapu Group, 21°23'S 174°55'W; AM R.111247, Apaiang Island, Gilbert Islands, 01°51'S 172°58'E; NTM R.13991-95, Koro Island, Fiji, 17°20'S 179°25'E: NTM R.13996-97 Yanduataba Island, Fiji, 16°50'S 178°18'E; NTM R. 13998, Upolu Island, West Samoa, 13°55'S 171°45'W; NTM R.13999, Tarawa Island, Gilbert Islands, 01°30'S 173°00'E.

Remarks. The chromosomes of *Gehyra oceanica*: A chromosomal analysis of *G.oceanica*, based on specimens collected from throughout the range of this species (Fig. 1), revealed chromosomal uniformity. The mitotic cell (Fig. 2a) is typical of the species, and is characterised by a diploid number of 2n=42 and a generally acrocentric karyotype (except for chromosome pair 14 which is metacentric).

The chromosomes of an undescribed species of *Gehyra* identified by King (1984a) as *G. oceanica*, and found on the Papua New Guinea mainland are shown in Figure 2b and King (1984a: Figs 1a, 1c, 2a). This 2n=44 karyotype is similar to that of *G. vorax* in terms of chromosome number and karyotype morphology. However, it differs substantially from that species in the quantity and distribution of heterochromatin in the genome and in chromosome arm lengths (see King 1984a: Fig. 2a, 3b). This form is described as a new species below.

In a broader evolutionary context, it is noteworthy that the great diversity in chromosomal and morphological characteristics present in *Gehyra* is found in Australia and islands closely associated with the Australian land mass (King 1979, 1984a). The species with the broadest distribution, *G. oceanica*, is commonly found on boats and in cargo on ships, and much of its present day distribution throughout the network of island chains can be attributed to passive introduction by Caucasian, Polynesian and Melanesian traders. Past tectonic activities allow for no other explanation than this. It is however noteworthy that the presence of *G. mutilata* on Madagascar, India and the Indonesian islands to the north of Australia, where populations are isolated by vast geographic distances, provides an inter-

esting contrast and could possibly reflect a relict Gondwanaland distribution if these populations are conspecific. In fact both chromosomal and immunogenetic evidence (King 1987) suggest that the Gekkonidae arose in Gondwanaland, a feature which would ex-

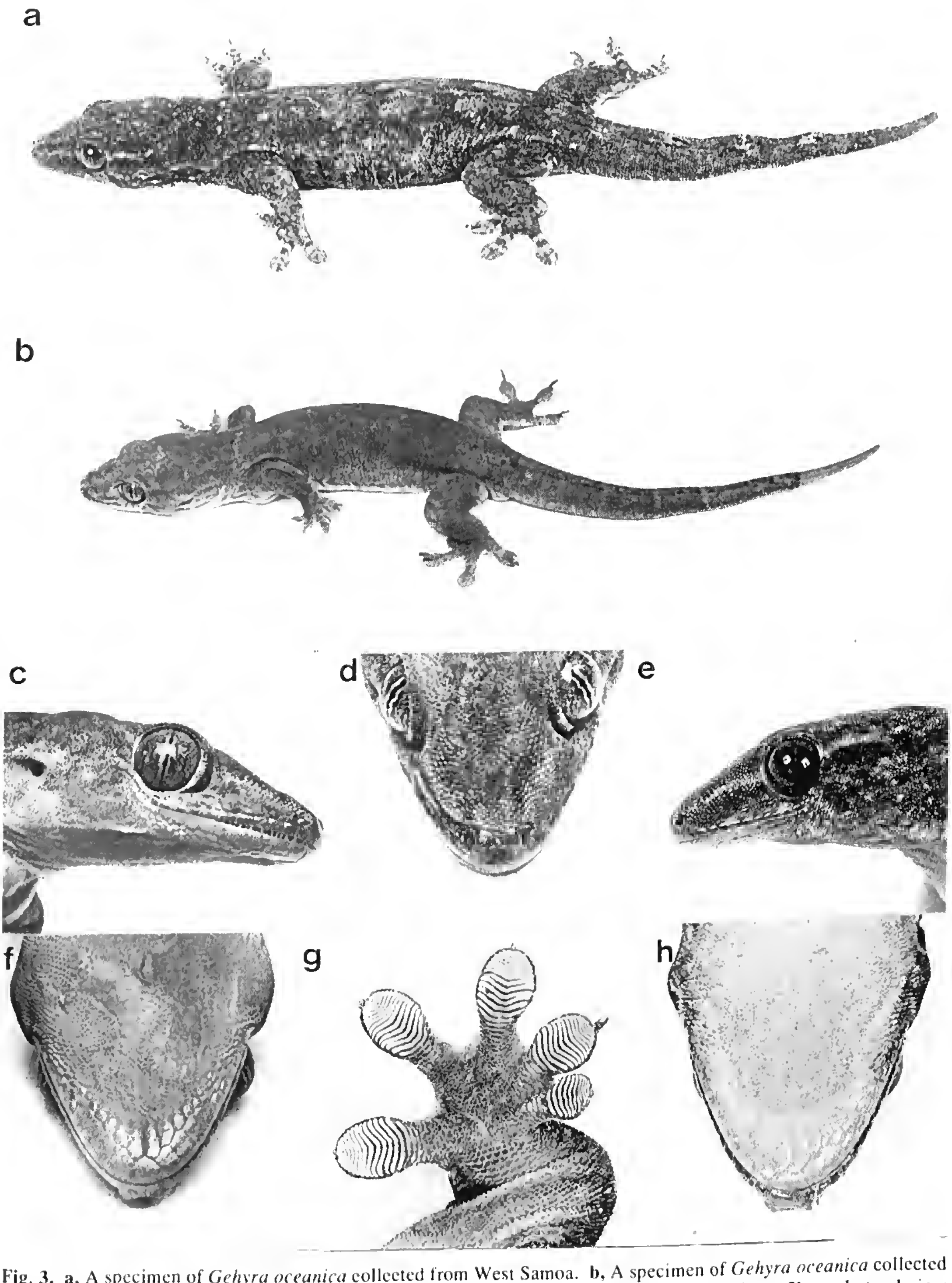


Fig. 3. **a,** A specimen of *Gehyra oceanica* collected from West Samoa. **b,** A specimen of *Gehyra oceanica* collected from Fiji. **c,** Lateral view of the head of specimen 2h. **d,** Dorsal view of the face of specimen 2b. **e,** Lateral view of the head of specimen 2a. **f,** Ventral view of the head of specimen 2b. **g,** Ventral view of the right hind foot of specimen 2a. **h,** Ventral view of the head of specimen 2a.

Table 2. Morphometric and meristic characteristics of *G. membranacruralis*, *G. oceanica* and *G. vorax*. Measurements are in mm. Measurements for *G. vorax* are derived from a single specimen. Tail lengths were measured from original tails only. (SD = standard deviation)

CHARACTERISTICS	*G. membranacruralis* n = 7 mean	SD	range	*G. oceanica* n =90 mean	SD	range	*G. vorax*
Snout-vent length	114.0	6.2	103.0 - 123.0	76.9	8.8	50.0 - 101.0	158.0
Tail length	102.0	0.0	- -	70.3	10.6	51.0 - 90.0	-
Forelimb length	32.0	2.4	27.8 - 35.0	21.4	2.7	14.4 - 27.9	46.0
Hindlimb length	41.5	2.7	38.9 - 46.0	27	3.8	15.4 - 34.5	52.0
Head width	20.3	2.0	16.7 - 22.3	13.3	1.7	8.6 - 19.2	30.2
Head depth	12.5	1.2	10.3 - 13.6	8.5	1.2	5.6 - 12.1	18.1
Ear-snout length	25.9	2.0	22.8 - 28.3	18.7	2.4	10.2 - 25.3	37.2
Nostril-snout length	2.0	0.2	1.7 - 2.3	1.4	0.2	0.9 - 2.0	3.0
Eye-snout length	13.4	0.9	11.8 - 14.3	8.6	1.0	5.6 - 12.2	17.7
Postmental scale length	3.3	0.4	2.0 - 4.2	2.6	0.4	1.8 - 4.0	4.5
Number of scales between eyes	47.3	0.3	43.0 - 51.0	47.2	3.6	39.0 - 57.0	85.0
Number of internasal scales	3.1	0.4	3.0 - 4.0	3.9	1.3	2.0 - 8.0	3.0
Number of supralabial scales	13.3	2.9	12.0 - 15.0	13.0	1.1	10.0 - 16.0	14.0
Number of infralabial scales	11.5	0.0	10.0 - 13.0	11.9	1.1	9.0 - 15.0	12.0
Number of mid-body scalerows	155.6	0.8	146.0 - 165.0	153.1	9.1	132.0 - 179.0	202.0
Number of fourth toe, subdigital lamellae	19.0	3.2	15.0 - 23.0	14.5	1.1	12.0 - 17.0	21.0
Number of preanal pores	39.4	1.1	32.0 - 44.0	34.8	4.8	26.0 - 51.0	61.0
Number of postanal spines	2.8	2.7	2.0 - 3.0	3.4	0.7	2.0 - 6.0	3.0
Tail length to snout vent length ratio	1.1	2.7	- -	1.1	0.2	0.9 - 1.5	-
Head depth to head width ratio	1.6	4.4	1.6 - 1.7	1.6	0.1	1.4 - 1.7	1.7
Head depth to ear-snout length ratio	2.1	0.4	1.7 - 2.4	2.2	0.2	1.1 - 2.5	2.1
Postmental scale length to snout-vent length ratio	35.3	0.2	28.8 - 37.7	29.9	2.8	23.8 - 38.6	35.1
Eye-snout length to ear-snout length ratio	1.9	0.0	1.6 - 2.1	2.2	0.2	1.2 - 2.3	1.7
Ear-snout length to snout-vent length ratio	4.5	0.2	4.2 - 5.4	4.2	0.6	3.6 - 8.1	4.2

plain the unusual distribution of the believed ancestral 2n=44 karyomorph of *Gehyra* in isolated pockets on the Australian mainland and Papua New Guinea, and slightly derived forms of this karyomorph on Fiji and in New Guinea (King 1984a).

Morphological Variation in *Gehyra oceanica*: A detailed morphological examination of 90 specimens of *G. oceanica* corroborates the uniformity of this species throughout its Pacific basin distribution (Fig. 1). That distribution extends from the Marquesas Islands in the east to the coastal islands bordering West Irian and Papua New Guinea in the west. There is no evidence to suggest that *G. oceanica* occurs on the New Guinea land mass at the moment, although its introduction must be imminent.

The morphological characteristics suggest that the island populations of this species which we examined are conspecific. These measurements are summarized in Table 2. This finding is supported by the chromosomal analysis described above. While some variation in back pattern is found between populations (Fig. 3), there appears to be no consistency in this character. However, it should be noted that *Gehyra* specimens collected from certain island populations were chromosomally and morphologically distinct and may be undescribed species (King, unpublished data).

Gehyra membranacruralis sp. nov.
(Figs 4-6)

Gehyra oceanica - de Rooij 1915:44; Whitaker *et. al.* 1982:42.
Gehyra vorax - de Rooij 1915:45-46; Whitaker *et. al.* 1982:42.

Type material. HOLOTYPE - NTM R.13746, male, Port Moresby, Papua New Guinea, 09°30'S 147°07'E, 1982, coll. D. Black (collected from University building wall). PARATYPES - PAPUA NEW GUINEA: NTM R.13744-45, 2 males, Port Moresby, 09°30'S 147°07'E, 1982, coll. D. Black, from University building walls; PNGM 22811, male, Mount Diamond, near Port Moresby, 09°30'S 147°07'E; PNGM 23176, male, Brown River, 09°20'S 147°30'E.

Diagnosis. *Gehyra membranacruralis* is distinguished from other Papua New Guinea *Gehyra* by a combination of characters. *Gehyra baliola*, *G. interstitalis*, *G. leopoldi*, *G. mutilata*, *G. papuana* and *G. variegata*

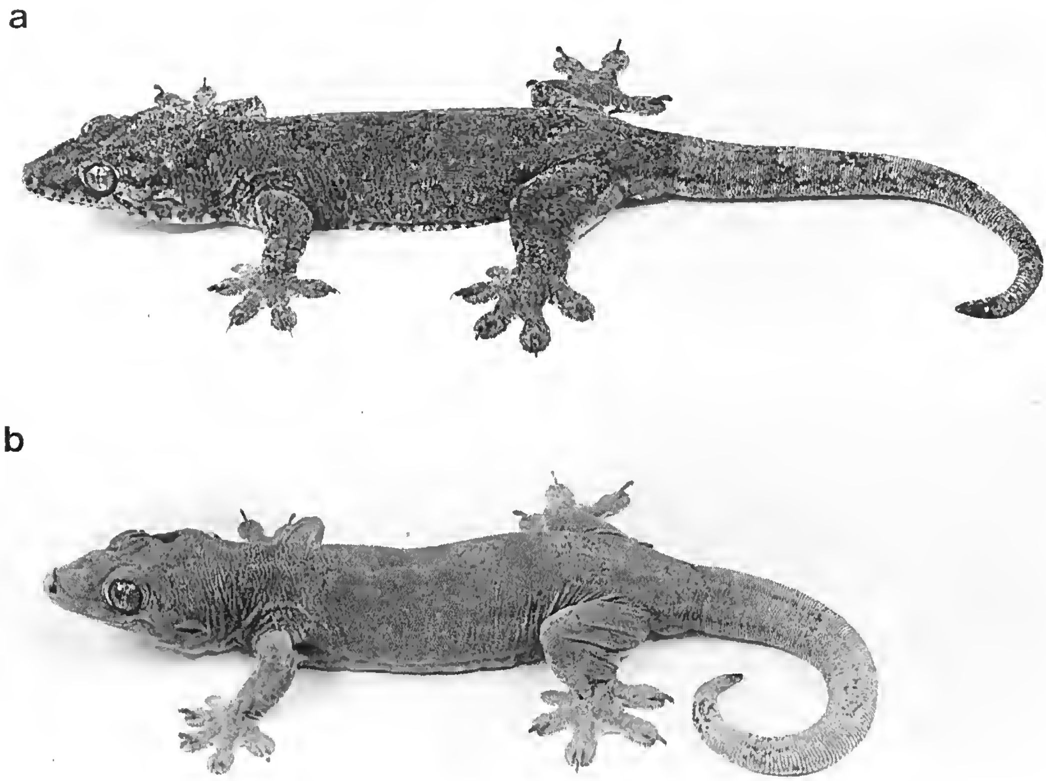


Fig. 4. a, The holotype of *Gehyra membranacruralis* in life. Note dark colouration. b, The holotype of *Gehyra membranacruralis* in life. Note marked fading in back pattern in different light regime.

have divided subdigital lamellae on the dilated section of the fourth toe, whereas those in *G. membranacruralis* are undivided. In addition, *G. interstitalis*, *G. leopoldi*, *G. papuana* and *G. variegata* are smaller, being usually less than 80mm in adult snout-vent length. *Gehyra baliola* and *G. mutilata* have a tail which is roughly triangular in section (rather than round to ovoid), due to the presence of enlarged lateral scales. *G. baliola* also possesses a characteristic 'U' shaped rostral scale. *Gehyra oceanica*, like *G. membranacruralis*, has undivided subdigital lamellae, nevertheless it is smaller in adult snout-vent length (50-101mm vs 103-123mm) and possesses only rudimentary webbing, directly behind the knees and between the toes. The Moluccan species *G. marginata* (holotype examined), is distinguished from *G. membranacruralis* by having anterior and posterior skin folds on the forelimbs and a tail that is roughly triangular in section.

Description of the holotype. Head: Width 16.7mm, depth 10.3mm, length 25.0mm. Snout 11.8mm long, from tip of rostral scale to anterior margin of orbit. Head covered by small rounded scales. 43 interorbital scales. Nostril surrounded by rostral, internasal, three posterior nasal and first supralabial scales. Rostral scale relatively deep, 1.8 times wider than high. Dorsal surface of rostral slightly gabled with middle of three internasals intruding down into rostral (Fig. 5a). Vertical median groove on rostral extending for 1/3rd of scale depth, from midpoint of dorsal surface. Midline horizontal groove across rostral scale. Nostrils separated by two large internasals and smaller middle internasal. 12L and 13R supralabial and 10L and 10R infralabial scales (Fig. 5d). Mental scale roughly triangular with intrusion of postmentals producing seven sides (Fig. 5b). Four postmental scales (anterior pair 2mm, posterior pair 2.4mm) posterior pair in contact with second infralabial scale (Fig. 5b).

Body: Dorso-ventrally compressed, heavily built (Fig. 4). Snout-vent length 111mm, tail length 102mm. Tail (original) ovoid to round in section, prehensile in life, terminating in a point. Single tranverse subcaudal scales. Dorsal surface covered by small juxtaposed rounded scales. Imbricate scales on

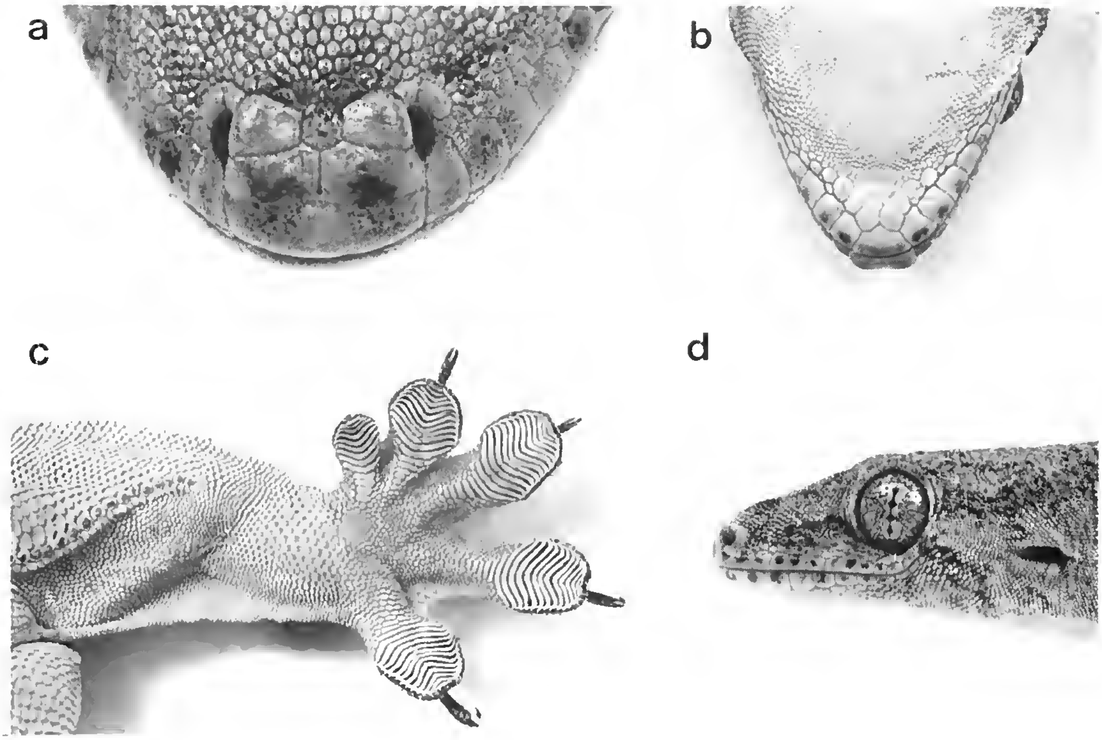


Fig. 5. a, Dorso-frontal view of the snout of *Gehyra membranacruralis*. **b**, Ventral view of the head of the holotype of *Gehyra membranacruralis*. Note the four postmental scales. **c**, Ventral view of the left hind leg of the holotype of *Gehyra membranacruralis*. Note the pronounced webbing between the toes and that at the back of the leg extending from foot to cloaca. **d**, Lateral view of the head of the holotype of *Gehyra membranacruralis*. Note patterning.

ventral surface larger and flatter than those on dorsal surface. 146 scales around circumference of abdomen in midbody. Lateral skinfolds on abdomen. No skinfolds on forelimbs. 20 subdigital lamellae on dilated section of fourth toe. Subdigital lamellae undivided (see Fig. 5c). Pronounced webbing between toes extends for some 1/3 of toe length. Hind legs larger and thicker than front legs. Forelimb 32.4mm long. Hindlimb 40.3mm long. Hindlimb with conspicuous webbing extending from base of fifth toe to cloaca then in continuous line to fifth toe of other foot. (Figs 5c and 6a). 37 preanal pores extending in a curved chevron, through midline apex, to near knees (Fig. 6a). Three postanal tubercles in cluster at base of tail, on each side.

Colouration: Background dorsal colouration of body grey brown with alternate dark brown granular blotches. These blotches extend onto limbs head and tail. On the tail they form five irregular bands (see Fig. 4a), and a most irregular lateral band which extends down the body to the forelimbs. The head shows pronounced dorsal and lateral mottling which becomes a pronounced darker eyestripe extending from the fourth supranasal through the eye and continuing to the nape of the neck where it meets the eyestripe from the other side. Black spots are found on the buff coloured supralabials and infralabials (Fig. 5d and 4a). The ventral surface of the body is buff coloured.

The same specimen can lose its colouration dramatically as illustrated in Fig. 4b. Here the dorsal surface becomes light grey with faint darker areas. The ventral surface remains buff coloured.

Distribution. The known distribution of *G. membranacruralis* is restricted to the Port Moresby-Brown river region of Papua New Guinea (Fig. 1). However, very few specimens are known and the distribution of the species could be more extensive than this.

Variation. Morphological and meristic characteristics of this species are summarized in Table 2. It is noteworthy that the holotype has two anterior and two posterior postmental

scales. Other paratypes have a single pair of larger scales in their place. This scalation characteristic appears to be variable.

Etymology. The name is drawn from the latin terms *Membrana*: "skin that covers special parts of the body" and *Cruralis*: "of the leg". *Membranacruralis* thus refers to the cutaneous skin fold found on the rear legs of this species.

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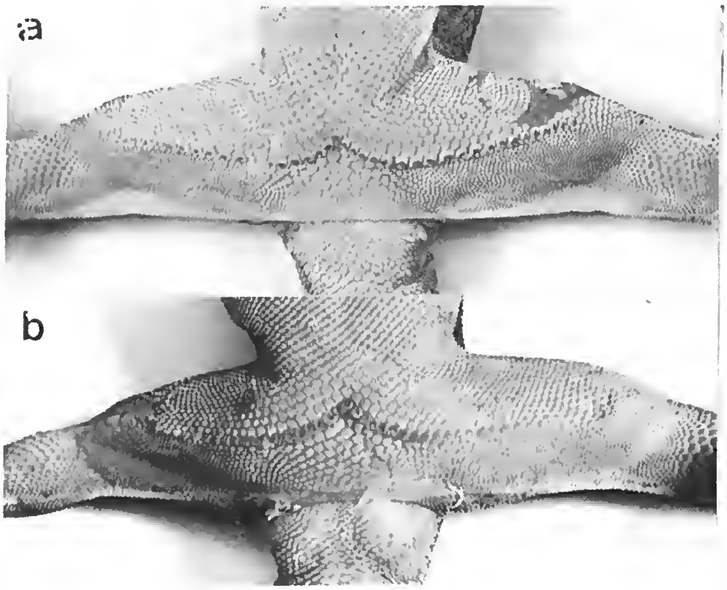

Fig. 6. **a**, Lateral view of the hind limbs of *Gehyra membranacruralis*. Note the continuous webbing extending from left to right foot. **b**, Lateral view of the hind limbs of *Gehyra oceanica*. Note the superficial webbing behind the knees. Compare to Fig. 5a.

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FOUR DOUBLE-ENDED *PERAHU LAMBO*

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ABSTRACT

The hull forms of four double ended Indonesian *Perahu lambo* are discussed. The *perahu lambo* is regarded as a borrowed western design but similarities of hull form to the traditional double ended *perahu soppe'* are noted.

KEYWORDS: *perahu, lambo,* sailing boats, maritime technology, Indonesia.

INTRODUCTION

Perahu lambo are the most westernised and amongst the most recently evolved trading sailing vessels in Indonesia. They are characterised by straight stem and stern post, straight keel, median rudder hung on the stern post and sloop or ketch rig.

The majority of *perahu lambo* have a counter stern but some have transom sterns and some are double-ended with a platform or gallery built over the stern.

In the past some fairly large *lambo* were built with transom stern or double-ended. In the late 1970's a few double-enders of about 40-50 tons burden were trading but these were all old boats (pers. obs.). The double-enders which are still trading in the late 80's are probably all under ten tons.

This paper is a survey of four small double-ended *perahu lambo*. Three of these are now in Darwin. The other, *Sama Biasa*, is in the collection of the West Australian Maritime Museum. Following the descriptions of these four vessels, similar double-ended craft of more traditional design from various places in Eastern Indonesia, usually called *perahu soppe', sope* or *sopek* are described. The possiblity that some characteristics of double-ended *lambo* design are derived from *perahu soppe'* is discussed.

Lines, sail plans and construction details of the four *perahu lambo* are presented but *perahu soppe'* are described only in a generalised manner. I hope that it will be possible to take lines off and survey thoroughly some *perahu soppe'* before they completely disappear.

Two of the vessels described in this paper: *Sejarah Islam* and *Wantoramata III* are from neighbouring islands in the Tukang Besi Islands which lie to the south-east of Buton (Butung) off the south-east of Sulawesi. Buton and the Tukang Besi Archipelago can be regarded as the centre of *lambo* building. Indeed *perahu lambo* have elsewhere been classified as *"Butung Lambo"* (Horridge 1981:66).

Sama Biasa, the *lambo* in the collection of W.A. Maritime Museum, is from Pepela on the island of Roti where many of the boatbuilders trace their ancestry to the Tukang Besi Islands (pers. comm. with Pastor Franz Lackner – Catholic Missionary to Roti and Savu, and communication with crews of boats from Pepela).

The fourth vessel *Sama Saja* is from Selaru, the most southerly of the Tanimbar Islands where there is no obvious connection with Buton or the Tukang Besi islands.

SEJARAH ISLAM

Sejarah Islam is a very small *lambo*, only 6.4m long and fine lined. She was built on Tomea in the Tukang Besi archipelago (5° 40'S, 124°E). She was used mainly for small cargoes and collecting voyages. Her owner, La Biru, said she had been sailed to Singapore, where she was probably smuggling rare birds from Eastern Indonesia.

In 1979 she was used to carry fish trapping equipment to the Macan islands (7°S, 121°E) for a season of trapping and salting fish. At the end of the season she was sold to the author and Mr Daniel Dwyer who sailed her to Darwin.

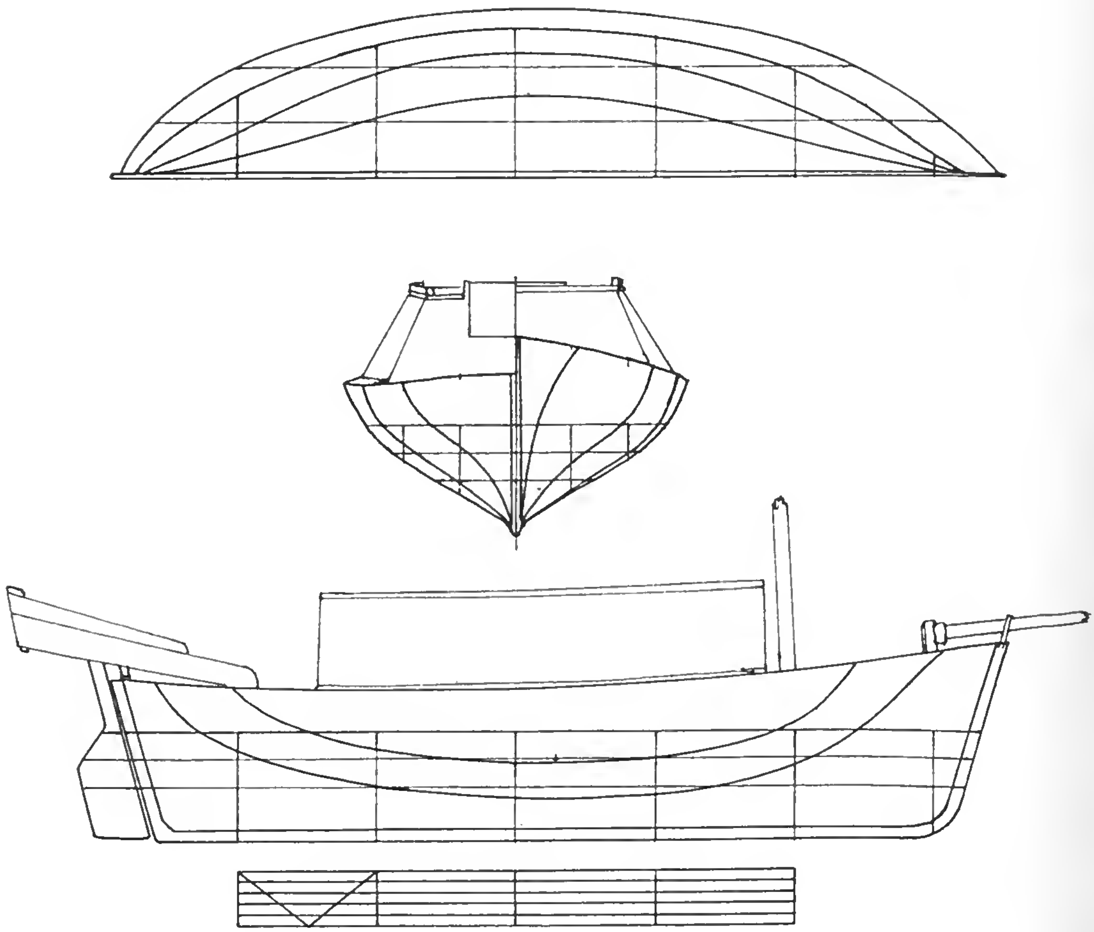

Fig. 1. Lines of *Sejarah Islam*

At that time her owner said she was eight years old. Others felt she might have been older.

There is some evidenee that she started life with an Indonesian lateen rig (*layar lete*). On the foredeek, under the bowsprit there was the ehoek for the heel of the spar of the *lete* rig. The *lete* rig has a spar held permanently at the bow so that it lies fore and aft and eannot be angled thwartships. Small open double-enders with this rig are common in the Tukang Besi islands, espeeially in the Bajo eommunities.

Sejarah Islam was later renovated in Darwin by Mr Miehelle Viet who sailed her to Gove in the Gulf of Carpentaria, baek to Sulawesi, Indonesia and returned to Darwin. Sinee then she has had a number of owners and has suffered periods of negleet. At other times she has been earefully repaired and maintained to keep her sound and still sailing.

Hull form. The lines of *Sejarah Islam* (Fig. 1) were taken off by the author in Darwin in 1981. As they have later been redrawn from a water damaged set of lines, there may be some inaeeuracy.

The profile on the sheer plan shows straight keel, straight stem and stern-post whieh are considered to be western introduetions (Horridge 1979:41). However the lines are quite distinetive and not obviously a copy from any western model. A more than superfieial resemblance to the New England "Block Island Boat" (Chappelle 1951:175, Fig. 64) has been suggested, but these boats certainly never reaehed Indonesia.

There is considerable deadrise (approximately 31°), and the bilges are slack. The turn of the bilge is harder forward where a shoulder of the bilge is carried into the bows and provides bouyaney in the section where the mast is stepped. The entry and run are

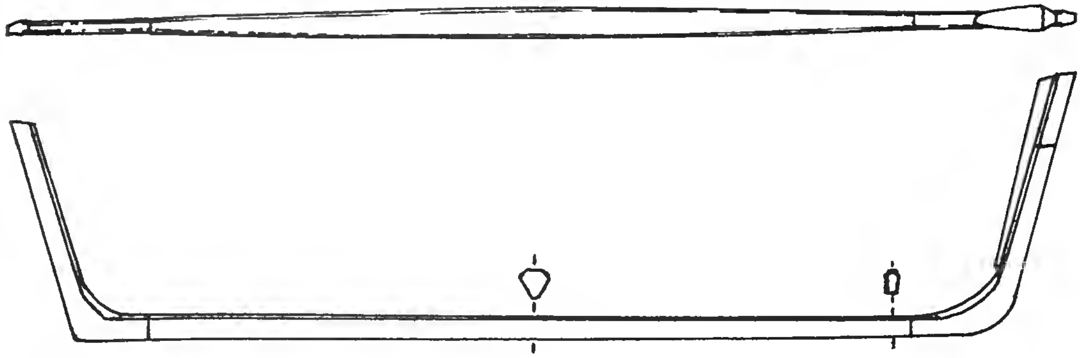

Fig. 2. Keel, stem and sternpost of *Sejarah Islam*

both slightly hollow. Above the water-line she is rather round and full aft.

Freeboard is low. In order to sail she must be well ballasted. With a cargo she would sail with only 200-300mm freeboard and on short voyages La Biru used to load her until her aft deck was at the water line. The inboard sloping cabin-sides effectively contribute freeboard and bouyancy. The cabin-sides and ends are as heavily planked as the hull.

Construction. The construction is heavy for such a small boat. Planking is 40mm or more in thickness. It is *Vitex pubescens* or *Vitex gofassus*, both dense tropical hardwoods.

The frames are not heavy by Indonesian standards, but moulded 80mm and sided 65mm they are still substantial for such a small vessel.

Construction of the cabin was similarly heavy and this made her crank unless properly ballasted. With the original heavy planked cabin roof she could hardly remain upright without ballast.

Like all Indonesian *perahu* she is shell constructed. The planks are carved to shape and fitted together with edge dowels at 200mm intervals. The ribs were fitted after the shell was planked-up. In small heavily planked vessels such as *Sejarah Islam* the shell is fairly rigid before the ribs are fitted. The ribs help to tie the planking together and take the strain from the shrouds; the lanyards of which are usually led directly to the top pieces (*taju*) of the frames. The planking was fastened to the ribs with wire nails and a few treenails. Michelle Viet and subsequent owners reported that almost all the nails were rusted through. She has been largely refastened and keel bolts have been fitted: originally she had no keel bolts. Larger *perahu* usually have keel bolts and more secure fastenings.

The keel is tapered towards the ends so that it is widest midships. Below the garboards the keel has a "V" section. Near the ends where the stem and stern posts are mortieed on, the keel has a rectangular section (Fig. 2). The stern post is a single grown timber with a crook forming the angle between keel and stern post. The stem is a similar crooked timber but this timber does not reach the top of the planking, a short piece of timber butted on forms the top of the stem. The two parts of the stem were not joined but both were fastened to an apron. The upper portion of the stem was only lightly fastened to the apron and had no structural function.

The Rig and Sail Plan. The original rig was set on a fairly tall mast that was both raked and curved aft (Fig. 3). The sail area was large. the mainsail was hoist well above the mast head on a gunter spar. The author recut the mainsail reducing the height by about 1 meter for the voyage to Australia. The sail area was still very adequate. Mast height and sail area have twice been reduced in Australia. The bowsprit is short for a *perahu lambo*.

There are no jaws on the boom. It lies to one side of the mast and is held to the mast by a strop. Reefing is achieved by unstropping the boom and simply rolling a portion of sail onto the boom.

Performance. *Sejarah Islam* performed well in company with other *perahu* though she could not be expected to keep up with larger vessels when reaching or running in a stiff breeze. She proved more weatherly than any *perahu* she met going to windward.

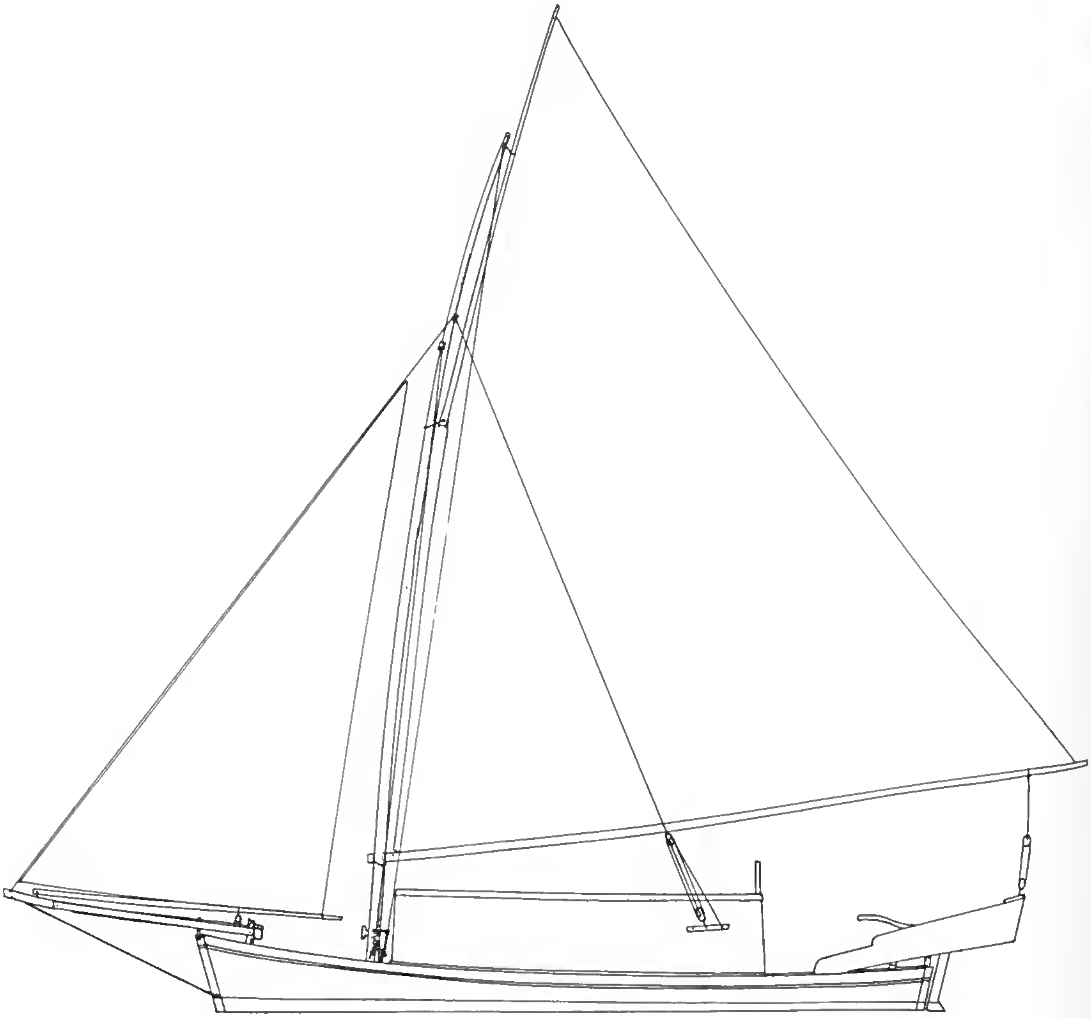

Fig. 3. Sail plan of *Sejarah Islam*

While Michelle Viet had her at Gove she won a race for cruising yachts and beat yachts of considerably greater size. She could not keep up with a good cruising yacht going to windward but when reaching she proved very competitive.

She is rather slow and unsure in stays.

WANTORAMATA III

This vessel was built in 1985-86 to be a fast example of her type. She was built at Kaledupa island (5°30'S, 123°40'E) northwest from Tomea where *Sejarah Islam* was built. The builders were natives of Kaledupa who spoke the local language. However Kaledupa formerly had a very large Bajo population. Bajo, some times called the Sea Gypsies are found in settlements all over coastal South east Asia. Traditionally they live in boats or in houses built on stilts over the sea. Most of the Kaledupa Bajo population have moved away, many of them settled at Pantai Mola on the neighbouring island of Wangi Wangi. The village of Buranga on Kaledupa where *Wantoramata III* was built is in fact not a Bajo village but looks like one because the houses are built over the water with stone causeways connecting them. *Wantoramata III* was built on beams suspended across the water between stone causeways. On her registration papers she is described as a *"Lambo Soppe"*. *Sope* the name of the large double-ended canoes of the Bajo is probably a cognate term.

While still new this vessel was purchased by Messrs Daniel and Bernard Dwyer who sailed her to Darwin.

Hull Form. The lines of *Wantoramata III* (Fig. 4) are very similar to those of *Sejarah*

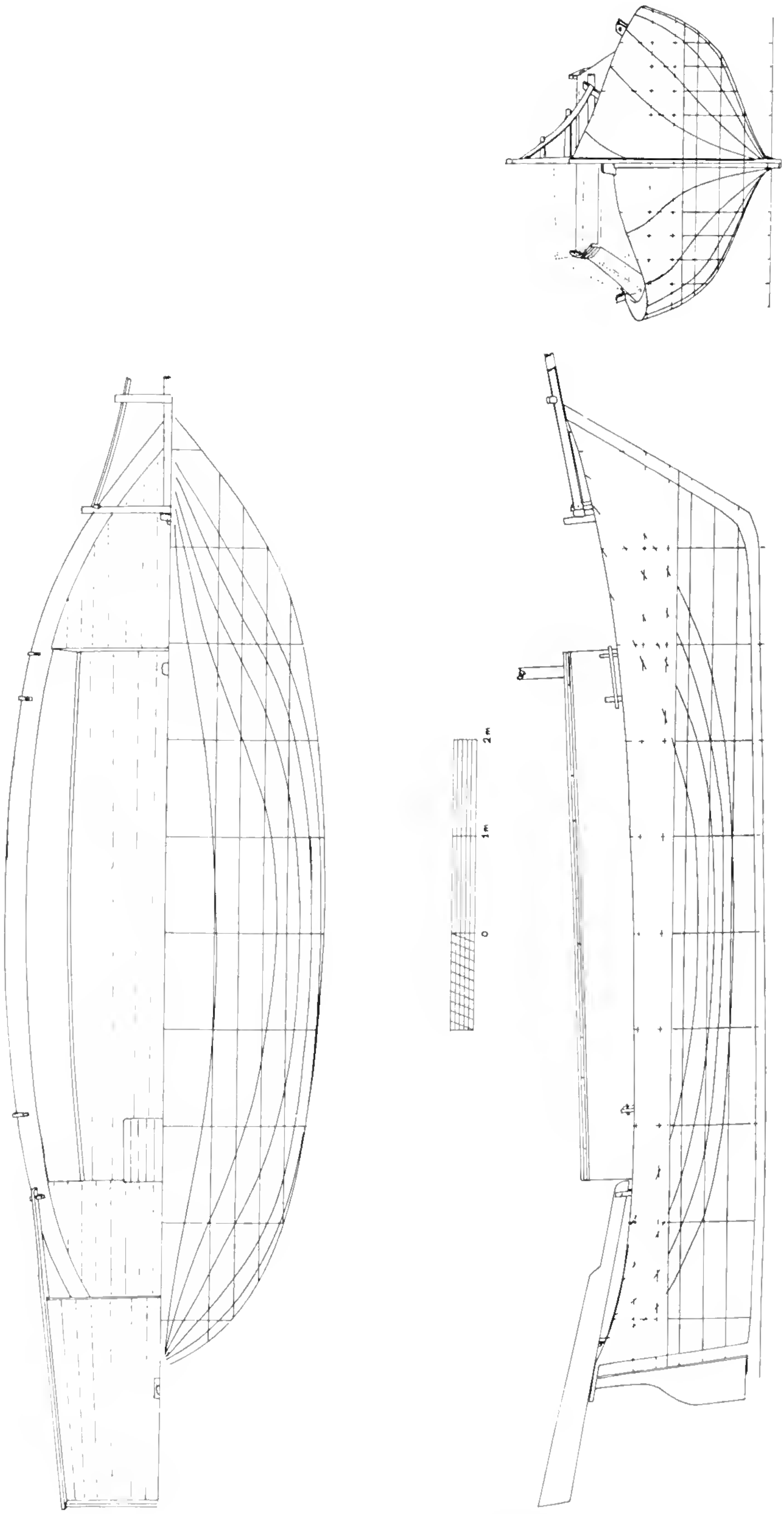

Fig 4. Lines of *Wantoramata III*

Fig. 5. *Wantoramata III* at Kaledupa

Islam. She has the same type of midship section showing deadrise, slack bilges and flared topsides. Freeboard is greater relative to other dimensions. The entry and run are long and a little hollow. Above the water-line the stern is rather round.

The stem is more raked than that of *Sejarah Islam*, while the stern post is more vertical. The near vertical stern post is typical for Kaledupa double-ended *lambo*. The greater rake of the stem is typical for *lambo* built almost everywhere in recent years. The oldest lambo usually have a plumb stem or nearly plumb stem. The average angle of rake seems to have increased gradually over the years (Horridge 1981:67; Burningham 1987:106).

Construction. The construction is lighter than *Sejarah Islam*. The planking is of about the same thickness but of a lighter timber, locally known as *kayu walu*. The ribs are mainly *kayu walu* (species not identified) and some *Intsia bijuga (kayu merbau)* a very hard dense timber. They are spaced at 220mm between centres. They are moulded 100mm and sided only 75mm, this is light but closely spaced framing for a vessel of this size by Indonesian standards. A similar proportioned *perahu lambo* from Bonerate, *Hati Mulia* (now in Darwin) has frames approximately 90x115mm at 300mm centres.

The workmanship on *Wantoramata III's* hull is excellent. Her planking seams are all completely tight and the frames are very exactly shaped and fitted. The bilge remains dry unless rainwater or spray enters through the deck or cabin.

The construction of the cabin is relatively light and the carpentry less sophisticated. There seems to be a different approach to the construction of the cabin which is sound but not built to the same standards as the hull. As with *Sejarah Islam* the cabin effectively contributes to the freeboard and bouyancy of the vessel when laden. With low initial stability she could be swamped if sailed without the cabin while carrying her tall sloop rig.

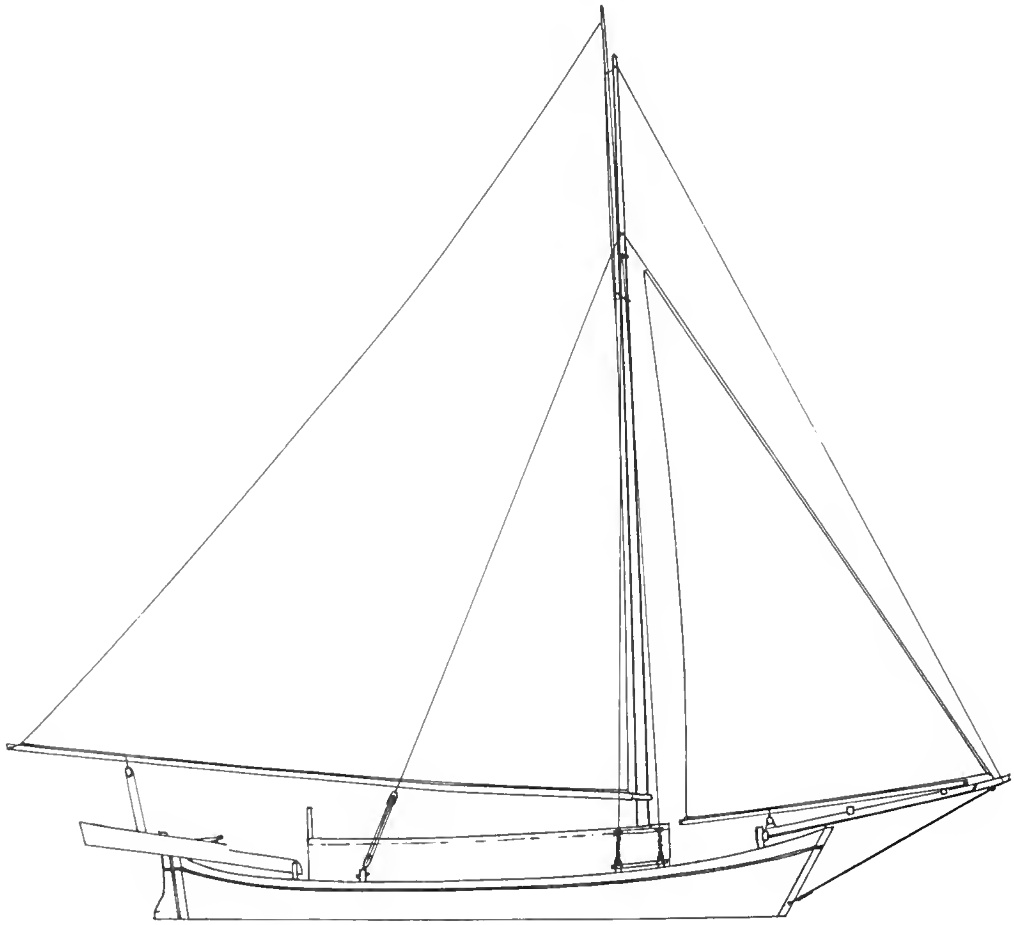

Fig. 6. Sail plan of *Wantoramata III*

Rig. The sail plan is similar to that of *Sejarah Islam* (Fig. 6). The mast is raked but straight. The main boom is very long and awkward to handle. It requires a preventer sheet to relieve the strain in the middle of its length in any real breeze. The jib is cut long in the leach so that the boom, if not supported by its topping lift, would hang below the bowsprit at the clew. This is normal for *perahu lambo* although it is less extreme in recent years than formerly when it was necessary for many *perahu* to sheet the jib's boom exactly fore and aft to go to windward.

Performance. Even with rather full cut sails and a draught of only 1m *Wantoramata III* is more weatherly than most *perahu* particularly in light winds with a head sea where her sharp lines and relatively light build give her an advantage.

Like *Sejarah Islam* she comes about slowly and is sometimes unsure in stays. Her rudder is rather small for manouvering. She requires ballast to sail.

SAMA SAJA

This vessel was built at Eliasa village on Selaru Island, the most southerly of the Tanimbar Islands in the South Moluccas. She is unusually beamy by any standards but can be regarded as representative of a class of small scruffy *lambo* of South Maluku (Moluccas) used for carrying small amounts of market produce, occasional sacks of cement and passengers who are frequently relatives of the owner. These vessels play a similar role to the family station wagon in rural Australia. *Sama Saja* was sailed to Bathurst Island, north of Darwin by her owner Simon Petrus Boinsera and five companions, three male and two female in 1986. One of the men, Dominggus John Kelmaskosu, had twice sailed to north

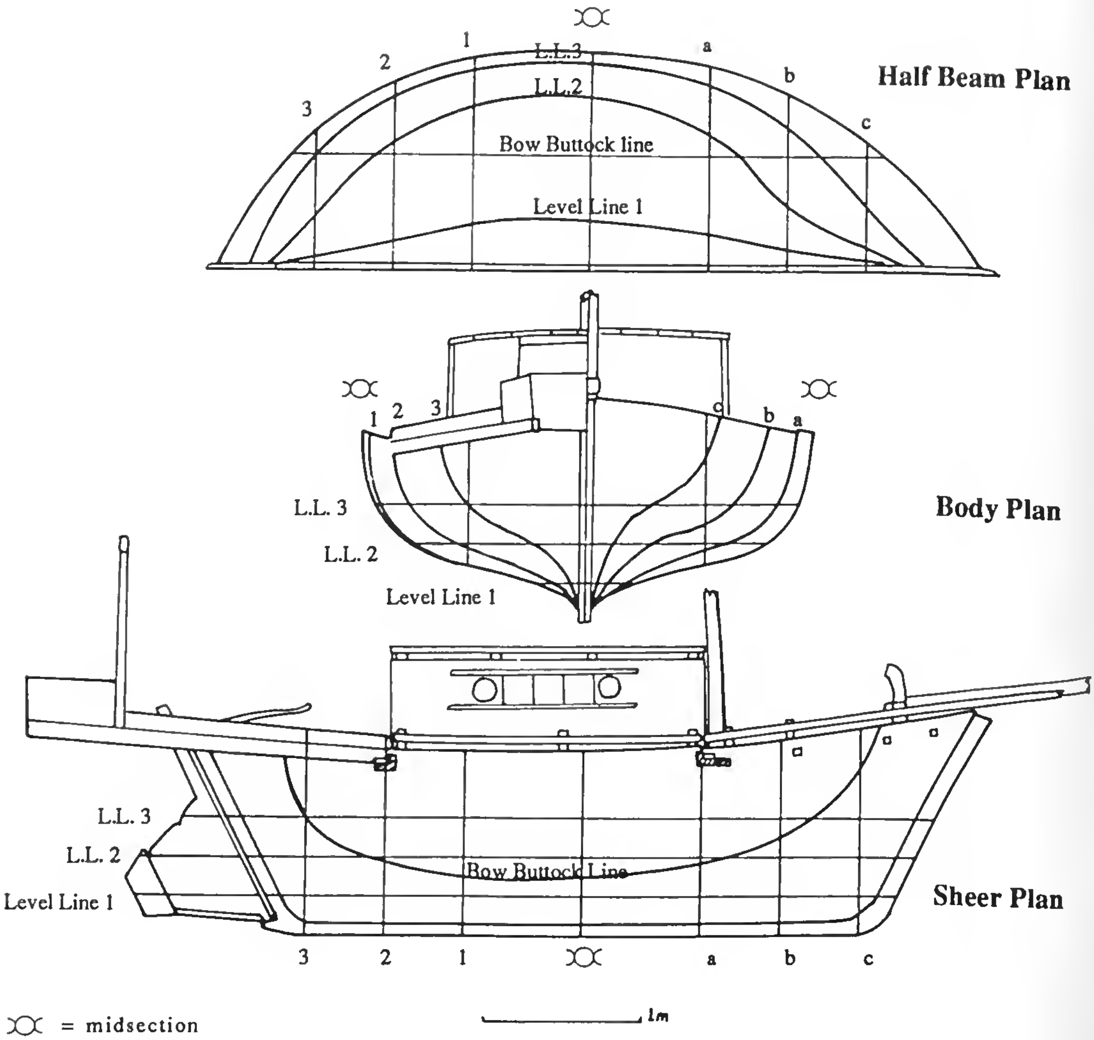

Fig. 7. Lines of *Sama Saja*

Australia in canoes during the 1960's and seemed to be the instigator of this voyage.

At Bathurst Island contact was made with local Aborigines and subsequently *Sama Saja* and her crew were apprehended by Australian Customs and immigration officers. *Sama Saja* was towed to Darwin where she was later purchased by the Museums and Art Galleries of the Northern Territory, and is now registered in the Southeast Asian material culture collections as IND 829.

Although very scruffy and unpainted except for a coating of asphalt and lime below the water-line she appears to be nearly new. Adze and axe marks on her timbers are quite clear. Simon Boinsera said she was two years old in 1986.

Hull Form. The lines are shown in Fig. 7. The beam of this vessel is quite extraordinary. The length beam ratio is 1:1.75 which must be almost unequalled in sailing vessels. The midsection is very different to that of the Tukang Besi Archipelago boats. She has moderate deadrise with very marked hollow. The turn of the bilge is fairly slack and continues all the way to the rail. The entry is very hollow below the waterline but she is fuller aft so that there is more forefoot than heel. A huge crude rudder compensates for the lack of heel.

The lines shown here are necessarily an approximation because the planking is not faired and the hull is not symmetrical. The lines shown are taken off the starboard side.

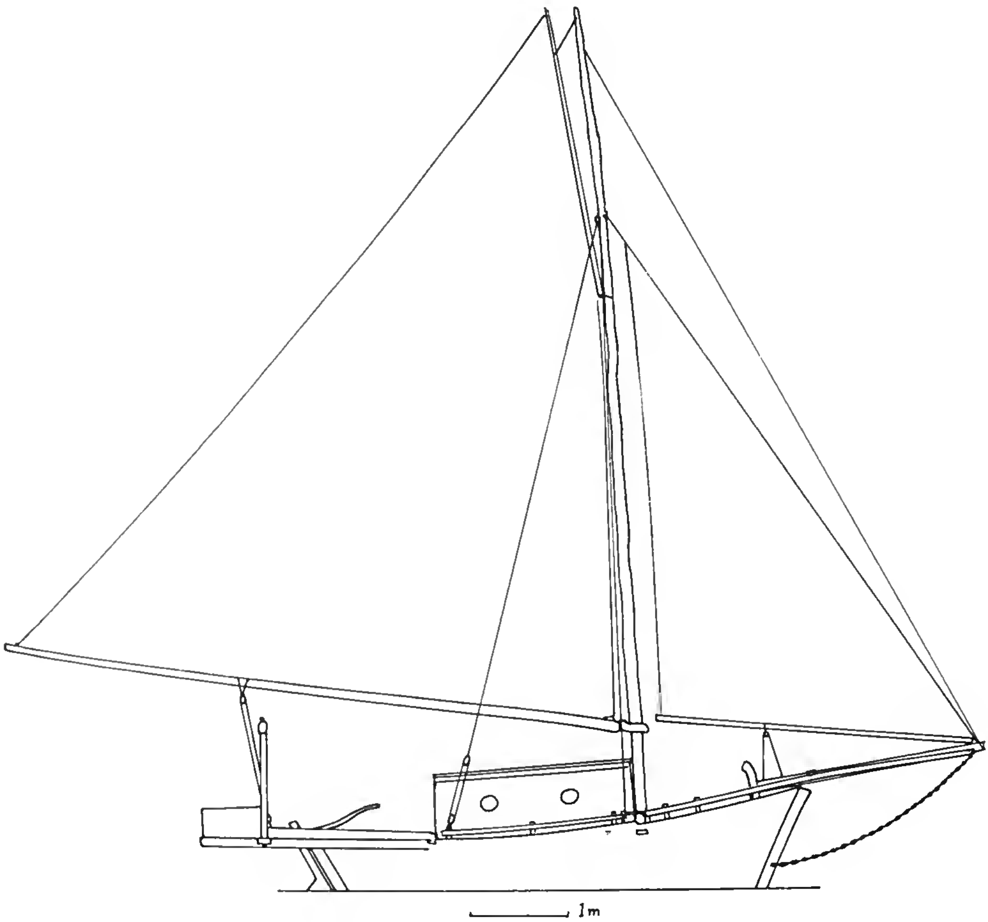

Fig. 8. Sail plan of *Sama Saja*

Construction. The planking is not of uniform thickness but much of it must be over 50mm thick. It is mainly *Vitex pubescens* or a very hard *Vitex gofassus*. The planks are irregular in shape and the run of the strakes is also irregular. Few planks are much over 1 meter in length. Some of the butts are at 45° to the run of the strakes.

Ribs are irregularly spaced, on average about 450mm between centres. In some cases they are roughly fitted tree limbs only faced to fit against the planking. Some of the floors are damaged by insect borers and were probably taken from an old vessel that was broken up. Every third floor has a keel bolt. There are not frames without a floor but the top futtocks are positioned midway between frames. The planking is fastened to the frames only with wire nails. Some of the ribbing clearly has very little structural value.

Stringers are no more than split saplings nailed in place. They only help to keep a cargo off the planking.

When purchased by the Museum, *Sama Saja* required pumping fairly frequently, preferably every 24 hours. She had been anchored in Darwin harbour in a place where she took ground on every tide. Considering this and the roughness of her build it is surprising that she could be kept afloat at all, far more that she could be left unpumped on a mooring for 48hrs.

The decks are appallingly scruffy and could never be made completely water-tight. The seams gape and the planks are inadequately fastened to inadequate beams. The wider seams were caulked with strips cut from rubber sandals known in Australia as "thongs".

One surprisingly sophisticated feature of the decking is the massive beams that are

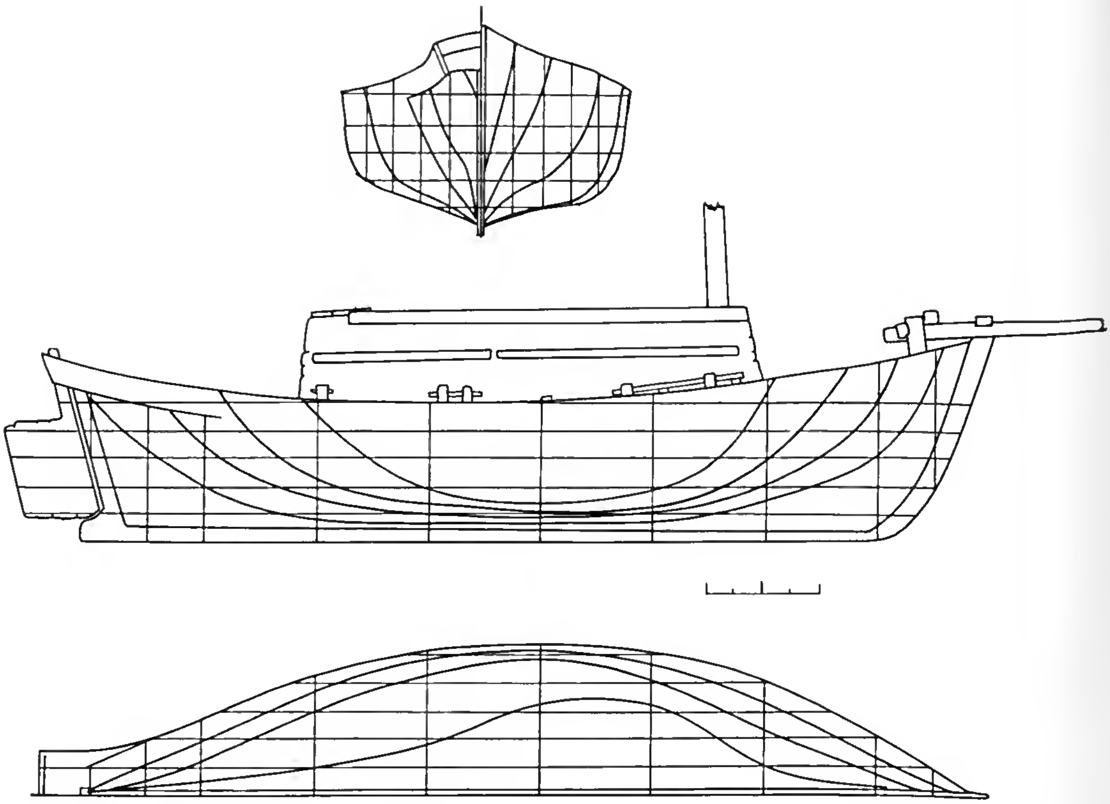

Fig. 9. Lines of *Sama Biasa*

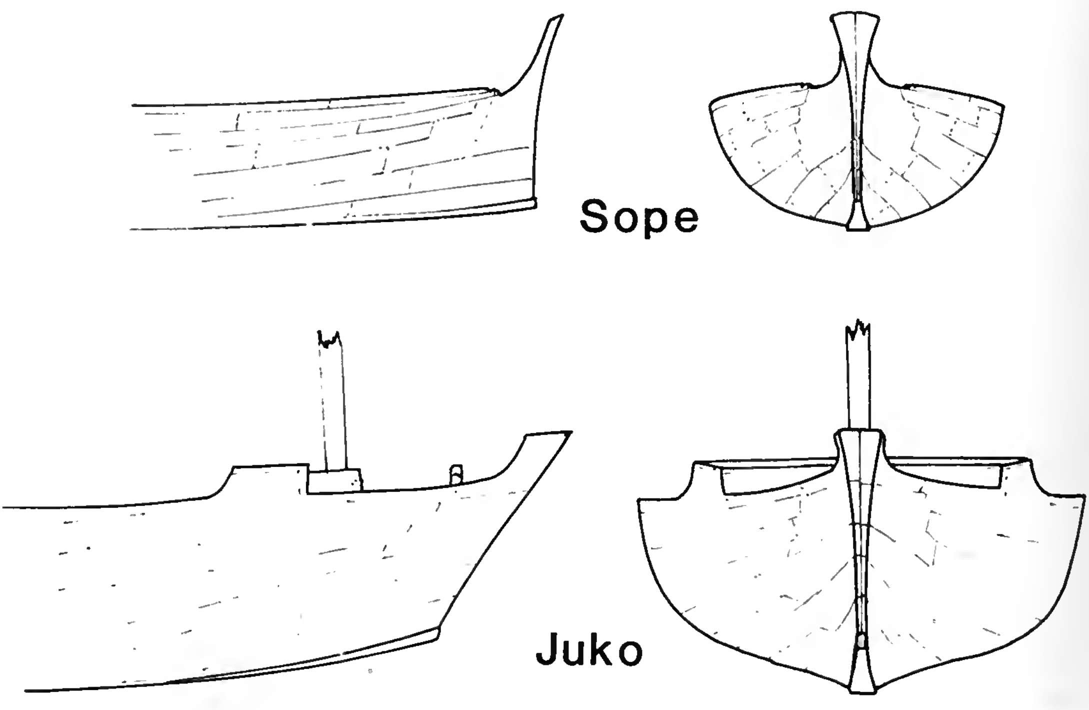

Fig. 10. Bows of Ende *perahu sopek* and *perahu juko*

made with "L" section to form a channel leading to the scuppers and prevent water running off the decks into the cabin.

Rig. The sail plan (Fig. 8) is fairly similar to that of *Sejarah Islam* and *Wantoramata III*. the jib is of lower aspect ratio and the rig projects further forward on the bowsprit and aft on the boom. In fact almost half the boom's length is aft of the stern post but this is necessary to drive such an ungainly hull. The mast was newly stepped for the voyage to Australia and was taller than the previous spar (pers. com. Boinsera).

The standing rigging was very poorly set up. The shrouds were set up with lanyards to a short rail nailed to two projecting top futtocks. The chain bobstay was set up too slack to stay the bowsprit, which was secured to the stem with a bolt and morticed through the samson post.

Curiously the mainsheet was rigged through dumb sheaves as a five part tackle: some *perahu* large enough to load fifty tons of cargo have only four part mainsheets. Some other details of the boat were quite whimsical. The cabin, although more roughly constructed than a packing case, has on each side two carefully sawn round port-hole-like apertures with sliding covers. These, along with the mainsheet cleat represent by far the most elaborate carpentry on the vessel.

Performance. The author was able to sail this vessel on three occasions. In sheltered water she proved fairly swift, quite able to make ground to windward and very handy – particularly fast in stays. Presumably a choppy head sea would severely prejudice her windward performance and she would be difficult to steer in good breeze. She was stiff without ballast of course.

SAMA BIASA

This vessel is fairly typical of a class of small double ender built at Pepela, Roti Island, Nusa Tenggara (10°20's, 123°25'E). It is possible that she is unusually full in the midsection and does not represent the best building seen at Pepela. These boats are used for collecting and fishing voyages to the islands and reefs lying south of Roti and inside Australian territorial waters (where traditional fishing by Indonesians is allowed according to a memorandum of understanding). These boats also trade around Roti and to Kupang, West Timor. Some make the voyage to Ujung Pandang (Makassar) to sell trochus shell, tortoise shell, trepang and other products of the collecting voyages.

Occasionally illegal voyages are made to the Australian mainland especially to poach trochus shell from the rich banks outside King Sound. *Sama Biasa* was apprehended on such an operation at Gregory Island in the Buccaneer archipelago. She was confiscated and donated to the Western Australian Maritime Museum.

Her lines were taken off by Mike McCarthy and Mike Pollard of the Western Australian Maritime Museum. Fig. 9 is traced from the lines as drawn by Mike McCarthy and Mike Pollard.

Hull form. The midships section shows little deadrise with slight hollow. There is a fairly hard turn to the bilge and little flare in the topsides. The run is unusually long and the full midsection short. There is some hollow in the entry below the water-line.

The hull form is significantly different from that of *Wantoramata III* or *Sejarah Islam*, particularly the midships section. The midsection coefficient (area of immersed midsection / limiting rectangle) of *Wantoramata III* is 63% while the midsection coefficient for Sama Biasa is 80%.

Although the hull forms are different there are many similarities of style. The cabin has a similar shape with inboard sloping sides and a flat top. On both *Sama Biasa* and *Wantoramata III* the mast is stepped through the cabin roof and this is not usual for *perahu lambo* which in most cases have the mast stepped forward of the cabin.

Ratios of length to beam for *perahu lambo* are consistently close to 3:1. *Sama Biasa* and *Wantoramta III* have length:beam ratios slightly lower than 3:1. *Sejarah Islam* has relatively greater beam, her length:beam ratio is 2.67:1.

Construction. *Sama Biasa* is fairly roughly constructed. Her planks are mainly *Vitex* sp. (*Kayu kolar*) and they are short and heavy. Frames are on average moulded and sided 90mmx90mm and the finish is not good.

Rig. *Sama Biasa* carried a gunter sloop rig.

PERAHU SOPPE'

Perahu sopek, *soppe'* or *sope* are names given to a number of similar small craft in

Eastern Indonesia. They are usually double-ended and similar in form to double-ended *perahu lambo*.

At Ende on the south coast of Flores a distinctive local boat made in several sizes is called *perahu sope*, *sope bajo* or *juko*. These vessels have no stem or stern post. The planking simply meet at the ends. *Perahu sope* are traditionally built up from a dugout although in recent years most are built with a keel. Small *sope* are sprit rigged and larger *sope*, which have decks and cabins, carry a gunter cat rig. Because there is no stem structure, there is no bowsprit or headsail. *Perahu sope* of Ende have a distinctive bow profile rather like that of South Sulawesi canoes. Other boats at Ende with the same stemless structure have a more raked bow profile, they are called *perahu juko* (Fig. 10).

On the island of Paloe off the north coast of Flores *perahu sope* of similar design and structure were built until recently. Some were built with outriggers others were rather deep hulled cargo vessels with no outriggers. Traditionally they carried a tilted rectangular sail (*layar tanja*).

At Oe Seli on the south coast of Roti a few *sope* still exist. Some have a dugout base and others have a keel. The lowest planks meet at the ends but there is a stem starting at the second or third strake. These boats are Indonesian lateen rigged (*layar lete*). All these types of *sope* have quarter rudders, they do not have a rudder hung on a stern post because there is no stern post.

The *sope* of Roti are very similar to other open lateen rigged boats with stem and stern post which are much more common on Roti and neighbouring Pulau Semau. These other boats which have stem and sternpost have large carved rudders hung on their stern posts.

The double-ended *lambo* of Pepela Roti such as *Sama Biasa* are scaled up versions of the lateen rigged boats.

Similarly *Wantoramata III* and vessels like her are scaled up from the open lateen rigged boats of the Tukang Besi archipelago. *Sejarah Islam* probably started life with a lateen rig and an open hold.

I am not aware of any stemless designs in the Tukang Besi islands but the double-ended *perahu lambo* there are designated *perahu lambo soppe* (on registration papers) which suggests that the design is taken from a *sope* design.

The various *sope* of Flores and Roti all have similar style and structure but have quite different midsections. The Roti *sope* are heavy with a full section (like *Sama Biasa*). The boats of Ende have moderate deadrise and very easy bilges. At Paloe there seemed to be two distinct styles. One with a round bottom and slab sides - more like a canoe, the other type had considerable deadrise and very flared topsides rather like the Tukang Besi boats.

C. Nooteboom in an account of boats at Ende (Nooteboom 1936, translated Horridge and Snoek) says:

> "The boats of the south coast are round in cross-section, those of the north have the form of a "V" although otherwise the various types of vessels are superficially similar in the two areas."

Sope or *sapa* were apparently more widespread and there were a number of distinct types in the 1930's. Nooteboom mentions *sope*, *sapa sangge*, *sapa bajo* and *sapa monda*.

DOUBLE-ENDED *PERAHU LAMBO* DESIGN DERIVED FROM *PERAHU SOPPE'*

Some of the main distinguishing features of double-ended *lambo* design are introduced western design. The straight stem and stern post structure, the stern-post hung rudder, and the rig are all introduced. Other less obtrusive but significant features seem to be derived from indigenous design. The hull profile, midsection and form are all like those of *perahu soppe'*. In some cases construction details could be derived from the built-up dugout design of the *soppe'*. The "V" section keel and structurally redundant upper stem of *Sejarah Islam* could be interpreted in this way.

There has been a tendency to regard *perahu lambo* as a crude or flawed copy of similar western fore and aft rigged vessels. It has been said that they sail badly (Gibson-Hill 1950:134; Horridge 1979a:37), that they are crudely modeled and crudely constructed (Gibson-Hill 1950:132; Horridge 1979a:32, 35; Hawkins 1982:129) and that they are unaesthetic (Gibson-Hill 1950:132; Hawkins 1982:123). Some of these comments seem to be motivated by a preference for more traditional craft which the *lambo* tend to replace. It has even been suggested that real sailors

would not select *perahu lambo*: that the West Sulawesi *lambo* (often called *perahu bago* or *palari*) which has a traditional Indonesian hull form is "altogether more of a sailor's boat" than the "Butung lambo" (Horridge 1981:16).

Most of these comments are applicable to vessels such as *Sama Saja* and perhaps *Sama Biasa* but disregard the evolved and successful indigenous hull form of well built vessels such as *Wantoramata III*.

NOMENCLATURE

The spelling of *perahu* types and Indonesian nautical terms, e.g. *lambo*, *sope*, *soppe*, *sopek*, *lete*, etc. conforms with the spelling used on vessel's registration papers where these have been seen by the author.

In other cases the spelling was provided by local boat owners. The form *soppe'* is from the Makassan and Bugis dictionaries of Cense and Matthes respectively and was suggested by Dr Campbell Macknight.

The spelling *lambo* equates with *Lambok* in Gibson-Hill (1950) and Hawkins (1982) and *lete* equates with Gibson-Hill's *leteh* (1950) and with *leti* used by Horridge (1981 and 1986) and Hawkins (1982).

GLOSSARY OF NAUTICAL TERMS USED IN THE TEXT

Clew

Aft lower corner of a sail

Deadrise

This term is fairly frequently used and understood, however comprehensive definition is difficult and uncommon. A survey of definitions in the literature produces some definitions that are simple but imprecise: "Vertical distance between keel and turn of bilge" (Palmer 1975:58), while others seem precise but virtually incomprehensible. For instance: "DEADRISE. Height to which a vessels frame rises from the horizontal as measured to intersection of a vertical, tangent to the molded depth distant point, with a line of frame extended from vessels keel;" (McEwen and Lewis 1953:124).

The following definition is an attempt to define deadrise as used in this paper and it is intended to conform with the use of the term by Howard I. Chapelle and David R. MacGregor.

Deadrise is an angle measured on the midsection or other cross-section of a vessel on the body plan (see Fig. 11). The deadrise angle at the midsection may be defined as the angle subtended at the point where the midsection outline meets the keel, by a line tangent to the midsection's outline and a horizontal line in the plane of the midsection (Fig. 10a,b,c). Traditionally this was usually expresed as inches per foot rather than degrees of angle.

In the run (q.v.) the deadrise can be the rise of a section's outline measured above the hollow of the deadwood area. In this case it is a question of visual interpretation rather than precise definition. An example of this usage is the concept of "constant deadrise" (Chapelle 1967:403).

Entry

The hull form forward of the midsection.

Flare

Angle outwards of the hull above the turn of the bilge. Shown on the body plan and sometimes on the buttock lines of the sheer plan near the bow.

Fore and Aft Rig.

A rig in which the principal sails will lie along or close to the fore and aft line of the vessel when they are not pushed out by the wind. Fore and aft sails are defined in contradistinction to square sails which will lie at 90° (square) to the vessel's fore-and-aft line unless pulled around by the braces. Fore and aft sails can be square or otherwise quadrilateral in shape while square sails are not necessarily square or quadrilateral in shape.

Well cut fore and aft sails will allow a vessel to sail closer to the wind than square rig in the circumstances that the sail area is adequate to drive the hull and the hull form gives enough lateral resistance.

Gunter rig.

A fore and aft rig on which a triangular sail is carried abaft its mast and has its head hoist above the mast head on a spar which lies approximately parallel to the mast when the sail is set. The upper part of the sail's luff is bent to the spar and the spar is hoist and lowered with the sail. See Figs 3, 5.

Gunter cat rig.

A single gunter sail carried on a mast stepped well forward. No headsail is carried.

Hard (turn of the) bilge

The turn of the bilge is described as hard if it occurs quickly and if it subtends a consider-

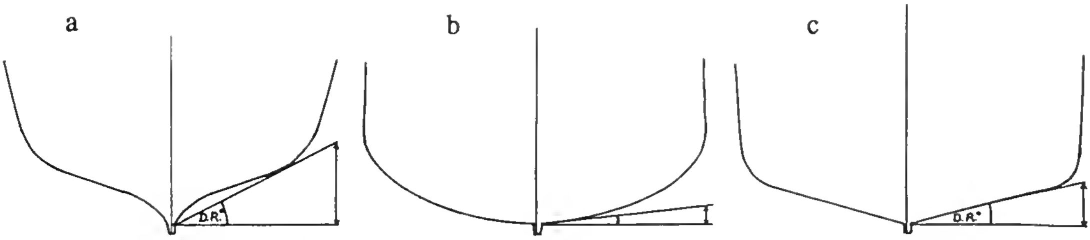

Fig. 11. Three examples of deadrise:
a. Deadrise angle shown on a midsection with hollow in the deadrise. There is a large angle of deadrise.
b. Deadrise angle on a midsection with an easy turn to the bilge starting close to the keel. The deadrise angle is small.
c. Deadrise angle on a midsection with straight rising floors or deadrise and a hard turn of the bilge. Deadrise is moderate.

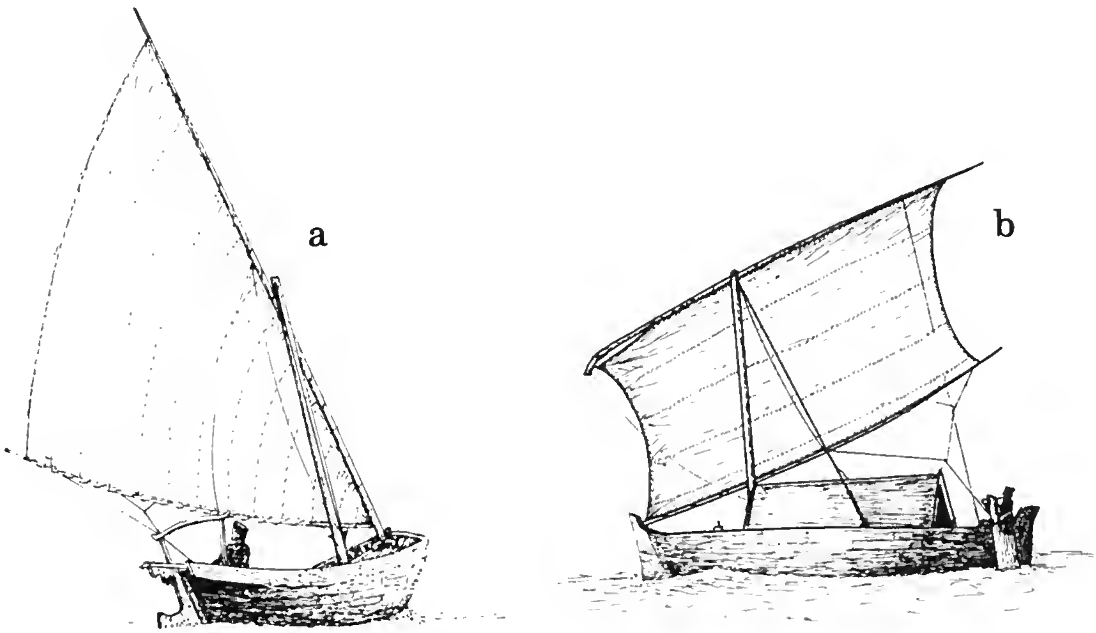

Fig. 12. a. Layar lete. Indonesian lateen sail on a Rotinese *perahu lete*
b. Layar Tanja. Indonesian tilted rectangular sail on a Paloe *perahu sope*

able angle e.g. Fig. 11a and 11c. A hard bilge is usually thought to confer stability and the power to carry sail to windward but may detract from speed and therefore windward ability.

Hollow

The lines of some vessel show hollow or concavity. Most commonly lower water-lines on the half beam plan will show hollow near the bow and stern. The body plan may show hollow deadrise (e.g. Fig. 10a). The quarter beam buttock line on the sheer plan occasionally shows slight hollow near the load waterline on fine-lined vessels with a counter stern.

Layar lete

Indonesian lateen rig. The sail has a boom laced on its foot. The entire length of the luff is laced to a heavy spar which lies fore and aft with its heel fixed in the bow of the vessel. When changing tack the sail and both its spars have to be taken over the top of the mast. Fig. 12a Roti *lete*.

Layar Tanja

A tilted rectangular fore and aft sail carried between a spar and a boom and handled rather like a *layar lete*. Considered a very powerful but unhandy sail. Fig. 12b.

Leach

Aft edge of a sail.

Luff

Forward edge of a sail.

Midsection

The widest and/or fullest section on the body plan. Usually located near the mid point of the vessels fore and aft line. A vessel which has the same section carried forward and aft is said to have a long midsection. A vessel in which the fullness of the midsection is quickly tapered away into the entry and run is said to have a short midsection.

Run

The hull form aft of the midsection.

Slack (or easy) bilge

A gradual turn of the bilge into the topsides, e.g. Fig. 10b.

Stays

A vessel is said to be "in stays" while her sails are flogging as she goes about from one tack to the other. If a vessel is fast and sure in stays she comes about readily when the helm is put down. A vessel which is slow and unsure in stays turns slowly in response to her helm and often needs considerable backing of her sails or use of oars to get her round to the new tack. If she fails to tack she is said to "miss stays".

Strake/Straik

A strake is a complete set or run of planks in a continuous line from one end of the vessel to the other. The planking of the hull is made up of a number of strakes and each strake is made up of a number of planks. The lowest strake is the garboard strake and the top strake is the sheer strake.

ACKNOWLEDGEMENT

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THE STRUCTURE OF JAVANESE *PERAHUS*

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ABSTRACT

The construction of a number of Javanese *perahu* types is described. A consistent four-straik structure is noted. A variety of bow and stern structures are described in which the stem and sternpost are either absent or structurally superficial. Structural affinity with ancient sewn plank designs is suggested.

KEYWORDS: Java, Indonesia, maritime archaeology, boat building, perahu.

INTRODUCTION

This paper presents lines, plans and construction details of three vessels from the Javanese tradition and a Malaysian vessel of similar construction. Typical features of the predominant Javanese *perahu* type - the *mayang* are described. Other Javanese and Madurese types are surveyed giving detail of some unusual stem and stern structures. The large, fully enclosed cargo carrying *perahu* of Madura are not included in the scope of this paper, nor is it intended as a comprehensive survey of Javanese and Madurese open boats.

The maritime traditions of Java and the large off-lying island Madura are part of the overall Southeast Asian maritime tradition but they can be treated as a distinct group of traditions (Macknight 1980:22).

The Madurese component is an important distinguishable element of this group and in considering the construction of traditional vessels some Madurese types show significantly different structure from the traditional types of Java.

The names of *perahu* types and Javanese nautical terms used here were mostly collected during a visit to Java in March, 1989. Translations and explanations of the terms were provided by local Javanese people and confirmed by rechecking later with other Javanese people of the same area. Very few of these words, nautical or otherwise, appear in the Javanese/English dictionary available to me (Horne 1974).

THE *MAYANG* TYPE *PERAHU*

The predominant *perahu* type of Java can be identified as the *perahu mayang* or "mayang type" (Horridge 1981:47-50, 82). Properly the name *mayang* belongs only to fishing vessels which are equipped with *payang* (purse-seine) nets but the term can usefully be extended to include all Javanese *perahu* with similar lines and construction to the traditional *payang* equipped *perahu mayang*. According to Horridge (1981:47) the *mayang* hull is characterised as "flat-bottomed with a large (sometimes very large) flat stem". They are not actually flat-bottomed in the strict technical sense that a barge is, but they have little or no deadrise in the midsection. The midsection is very distinctive and provides the principal distinguishing characteristic used in this paper. Typically there are four broad flat straiks forming a section with three chines. This feature can be seen in the lines of the vessels *Terima Kasih* and *Perawan* (Figs 1, 3, 7).

Another characteristic of the *mayang* type is the use of bulkheads rather than ribs (Horridge 1981:49). Not all *mayang* type are now built with bulkheads but bulkheads can be seen in the construction plans of *Terima Kasih* and *Perawan* (Figs 2, 4, 7). The bulkheads are luted and paid with resin as if to make them water-tight but there are limbers (holes)

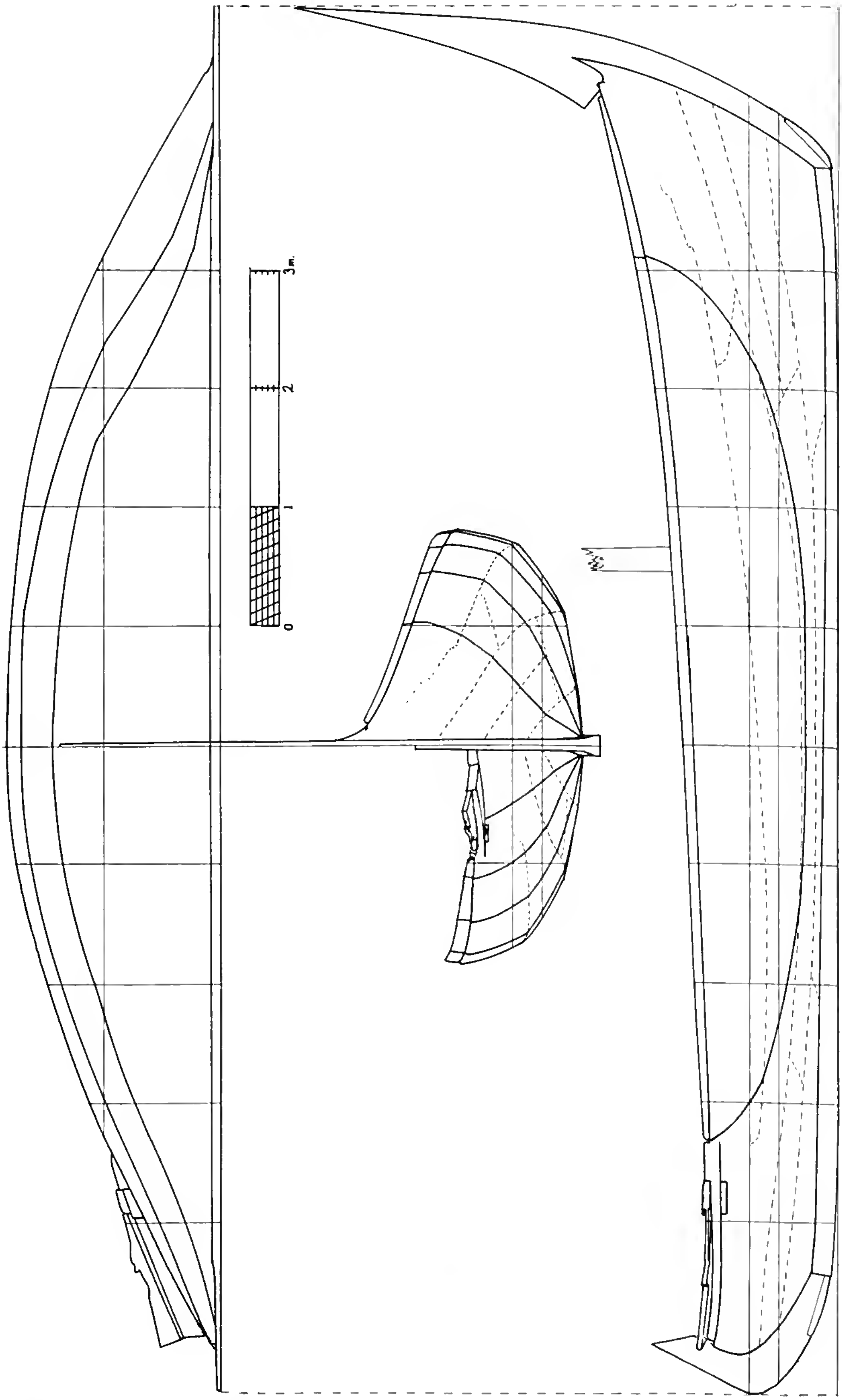


Fig. 1. Lines of *Terima Kasih*.

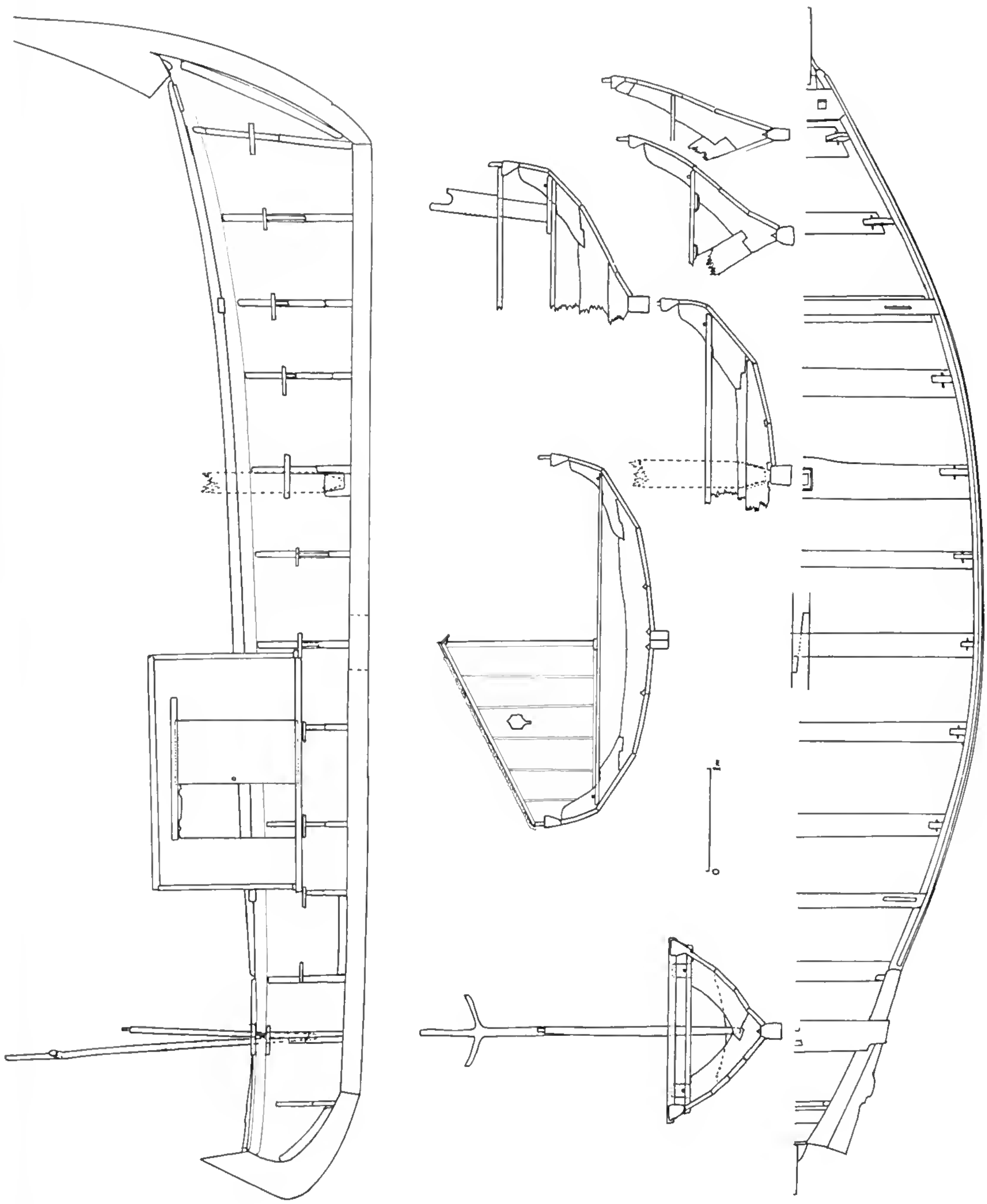


Fig. 2. *Terima Kasih*, construction diagram.

through the bulkheads to allow passage of bilgewater along the keel and first chine. Luting rather than caulking is used in the Javanese tradition; fibrous material, usually paper bark (*Melaleuca* sp.) is placed into the seams between timbers during assembly whereas caulking is served (hammered) into the seams after assembly.

Some *mayang* type vessels have stems which form large projecting prows and there are often similarly projecting stern posts. These form the distinctive prow shapes which identify many of the *mayang* types found along the Java coast (Horridge 1986:10-14). Some types have only small stems and sternposts and there are also vessels with the typical

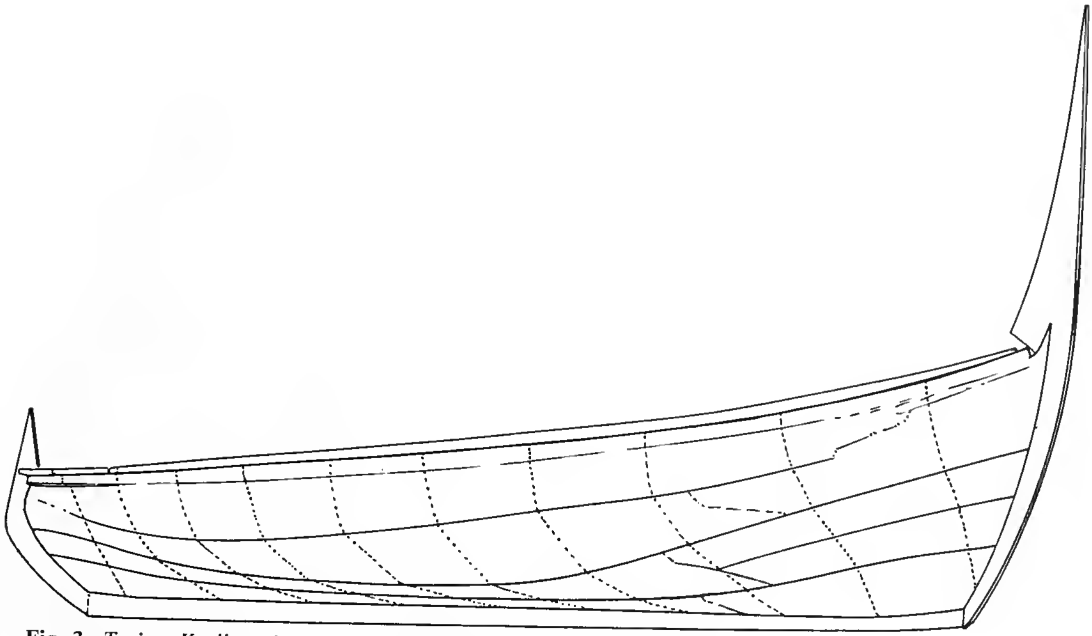


Fig. 3. *Terima Kasih*, orthographic projection showing run of straiks.

mayang midsection which have no stem or stern post; the planking simply meets at the ends of the hull (Fig. 8).

CONSTRUCTION OF JAVANESE *PERAHU*

There are a number of peculiar bow and stern structures used in the construction of the *perahus* and small craft of Java and Madura. In the following descriptions of these structures, where only a bow structure is detailed, it may be assumed that the stern structure is the same. There is a considerable range of sophistication in the boat building found along the coast of Java. At Jepara there are simple rafts formed of three logs dowelled together. Simple dugout canoes can be found in a number of places but in recent years availability of suitable logs for dugouts has been very restricted.

Planked-up dugouts are more common. Along much of the north coast of Java there is a more-or-less standard form for planked-up dugouts, although structure varies regionally. Like all Indonesian planked vessels they are shell constructed with edge-dowels holding the planks together. Characteristically these planked-up dugouts have absolutely straight flat sides through a long midsection. The bow and stern are moulded to meet the flat sides at an angle (Figs 9, 10), rather than curve gently into the midsection. Some traditional vessels from other parts of Indonesia have a similar hard angle at the bow and stern but the flat sides of the Javanese canoes seem to be unique (cf. Horridge 1979b:Figs 8, 9, 33; Burningham 1988:Figs 3, 7).

The structure of the planked-up canoes of Central Java is crude. The hard angle in the bow and the stern are formed where flat planks are butted together (Fig. 9). There is a stem-like structure made up of a number of horizontally layered blocks. The planks that form the bow and stern simply butt on to the stem piece and are each secured to the stem by a single skewed dowel. These vessels usually have a relatively large and heavy dugout base. They are normally fitted with a single outrigger carried to port on a single boom (Fig. 11). The best examples of this type are the *jukung* of Rembang, close to the border of East Java (Hawkins 1982:101-103).

In East Java, mainly in the area of Tuban, there are planked-up dugouts with similar hull form but more sophisticated construction (Figs 10, 12, 13). These are called *jatan* or *jatan walon* if they have a true dugout base. However there are many of the same hull form which have the dugout base reduced to a central plank or even a narrow keel, in which case they are called *jatan pedatan*; this apparently means *jatan* [i.e. dugout] that is not [a dugout].

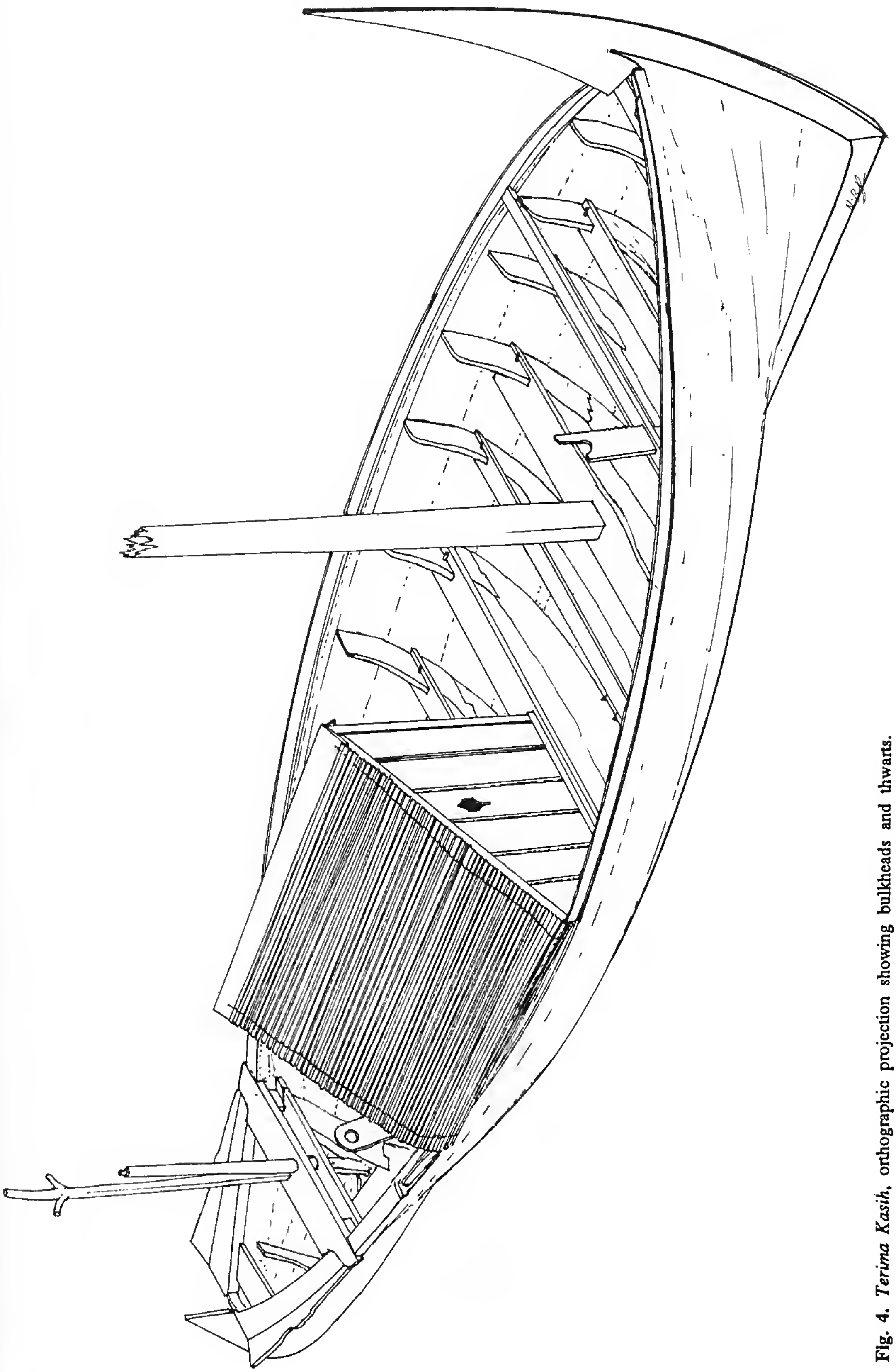


Fig. 4. ***Terima Kasih***, **orthographic projection showing bulkheads and thwarts.**

The structure shown in Figures 10, 12 and 13, is fairly typical for *jatan pedatan* but not all have the forked or wing stem-pieces. Some have the simple block stem-pieces found in central Java but the stem is raked so that the plank ends can be edge-dowelled to it (Fig. 14). The dowels which hold the planks together are all fitted with locking pins (Fig. 15).

Typically the turn of the bilge is carved into the plank which forms the lower part of the topsides. This plank is called *papan menteng* (*papan*=plank, *menteng*=pauneh). There are never any ribs. A number of thwarts and beams (usually six) are fitted. Small thwarts let through the hull help to hold the ends together.

Like the *jukung* of Rembang the *jatan* carry a small sprit rig but they are not fitted with outriggers to provide stability so their hull form is relatively wider and lower.

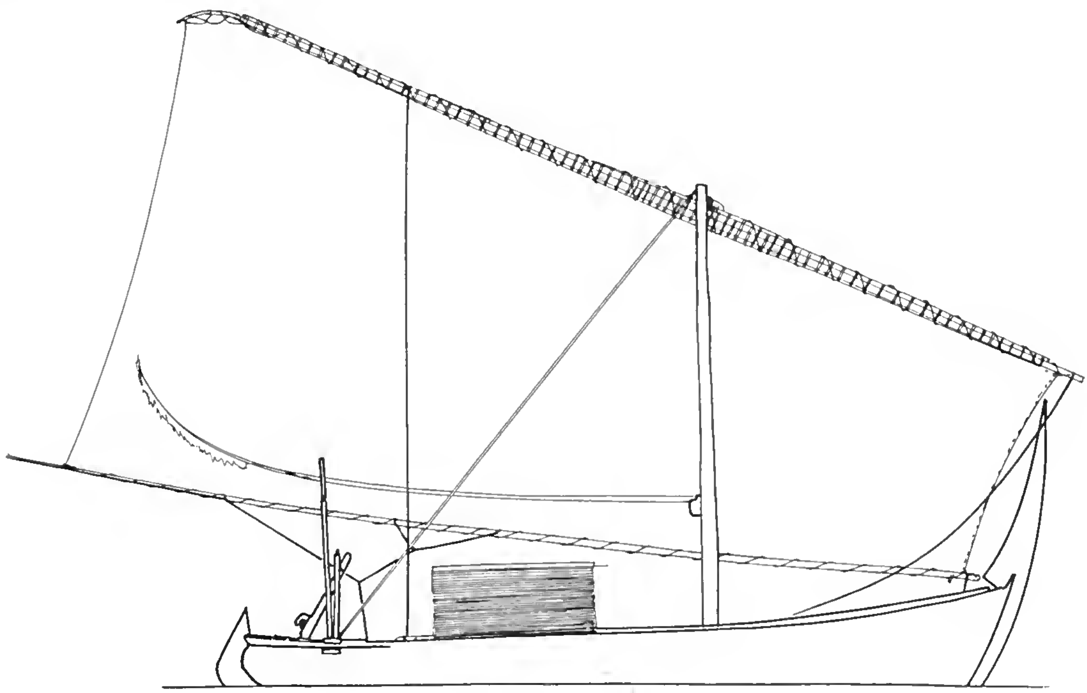
On Madura and the Java coast near Madura there are built-up dugouts belonging to the Madurese *Jukung* tradition. Their structure belongs to a very widely spread tradition called the "five part canoe" by Haddon and Hornell (1938:5) (see also Horridge 1987).

PLANKED BOATS

Stemless boats called *perahu jegongan* and *perahu condong* are found in the Indramayu area of West Java. The *condong* is a rare form of *jegongan* with a split prow (Fig. 16). *Jegongan* have the typical four-straik structure of *perahu mayang*. The planking simply meets at the bow and stern where it is held together by tree-nails (dowels) and it is also fastened to an apron-like piece *(serang)*. The *serang* is fitted after the planking is assembled, it is often shaped from a split tree trunk and is left fairly roughly shaped near the top (Fig. 25a). The prow and stern finials also have apron-like pieces inserted, these are separate from the *serang*. In the bow there is a small thwart let through the planking. In both bow and stern there are frames formed from grown forked timbers called *gading cempet* (pinched or squeezed frames). The ends of the *gading cempet* project above the rail forming bollards or bitts in the bow.

Although *jegongan* have the distinctive *mayang* four-straik shape they are frequently built with a greater number of straiks because of difficulty in acquiring suitably wide planks: Even so, the builders shape the vessels with three chines and consider the vessels to have four straiks or *jegong*. The four straiks are named *jegong dasar* (base straik), *jegong karon* (*karon* is rice cooking but not yet rising), *jegong telon* (third straik) and *jegong menteng* (pauneh straik).

Fig. 5. *Terima Kasih*, sail plan.



A moderately large *jegongan* at Eretan west of Indramayu measured 10.6 x 3.8 x 1.15m. This compares with typical large *mayang* measurements of 11-12 x 3.65 x 1.15m given by Horridge (1986:10). The *jegongan* has relatively greater beam but the immersed hull form is similar because the water-line length is the same as the overall length in the case of the *jegongan* which has plumb (vertical) ends.

At Eretan and nearby Parian there are many *jegongan* but the most numerous *perahu* there is another type with the *mayang* mid-section called *perahu compreng*. There are many *compreng* of the same size as the large *jegongan*, but the *compreng* are used only for fishing in local waters, whereas *jegongan* voyage farther and can be found along the Central Java coast, even during the west monsoon when heavy weather is most likely (pers. obs. March 1989). Most *jegongan* are now fitted with long shaft motors and carry a small auxilliary *lete* type sail (Fig. 29). Formerly they carried quadrilateral sails similar to that illustrated in Figure 5.

Perahu Kompreng, Compreng* or *Sompreng are *mayang* type vessels built and operated on the coast of west Java around Cirebon and Indramayu, and in the western part of central Java. They have high curved prows that give a characteristic *mayang* profile (Fig. 17), and they have the four-straik structure and form although there are frequently more straiks used if wide planks are not available. In the following description of the structure and illustrations a "classical" four-straik structure is assumed.

The bow is constructed with a stem which is morticed on to the end of the keel. The lower three straiks are fastened into a rabbett on the stem. The fourth straik terminates a little abaft the stem. The prow is built up from blocks of timber tenoned together which radiate from the forward ends of the fourth straik (Fig. 18). Perhaps this peculiar structure was once more elegantly moulded using selected grown curved timbers in a structure similar to the *jatan's* bow (Fig. 19). *Kompreng* are now built from straight planks and blocks bought from saw mills.

The stern structure is similar but there is only a very short stern post formed by an upturned end of the keel (Fig. 20). Only the first straik terminates on the stern post. The second and third straiks run out as stealers in

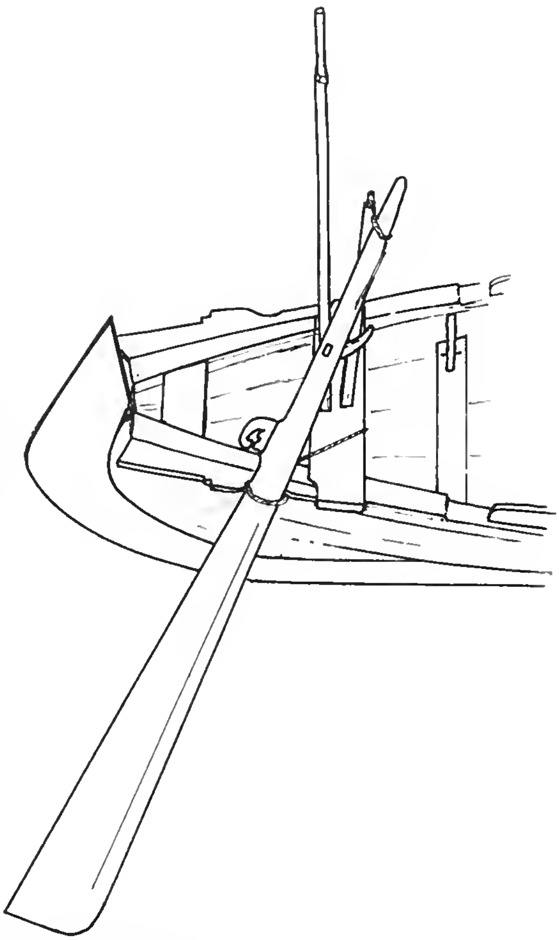


Fig. 6. *Terima Kasih*, orthographic projection showing rudder mounting.

the first straik and second straik respectively. The fourth straik is moulded into the stern finial in the same way that it is moulded into the prow. Some small *kompreng* have the stern finial built up from forked timbers, perhaps this was once standard both in the bow and stern.

The pieces that are tenoned together to form the sternpost and stern finial structure are fitted after the planking is in place, and an apron-like piece has been fitted (Fig. 21).

Perahu kompreng carry a three spritsail rig when reaching or sailing to windward. When sailing off the wind the mizzen is unstepped. The large Javanese rudder carried on the lee side (Fig. 6) confers resistance to leeway, which the hull lacks, only if there is sufficient sail area aft to prevent lee helm; hence the use of the mizzen (cf. Horridge 1981:Pl. 24).

Perahu Seroto are built in the same area as *perahu kompreng*, that is mainly around Cire-

Fig. 7. *Perawan*, lines and construction.

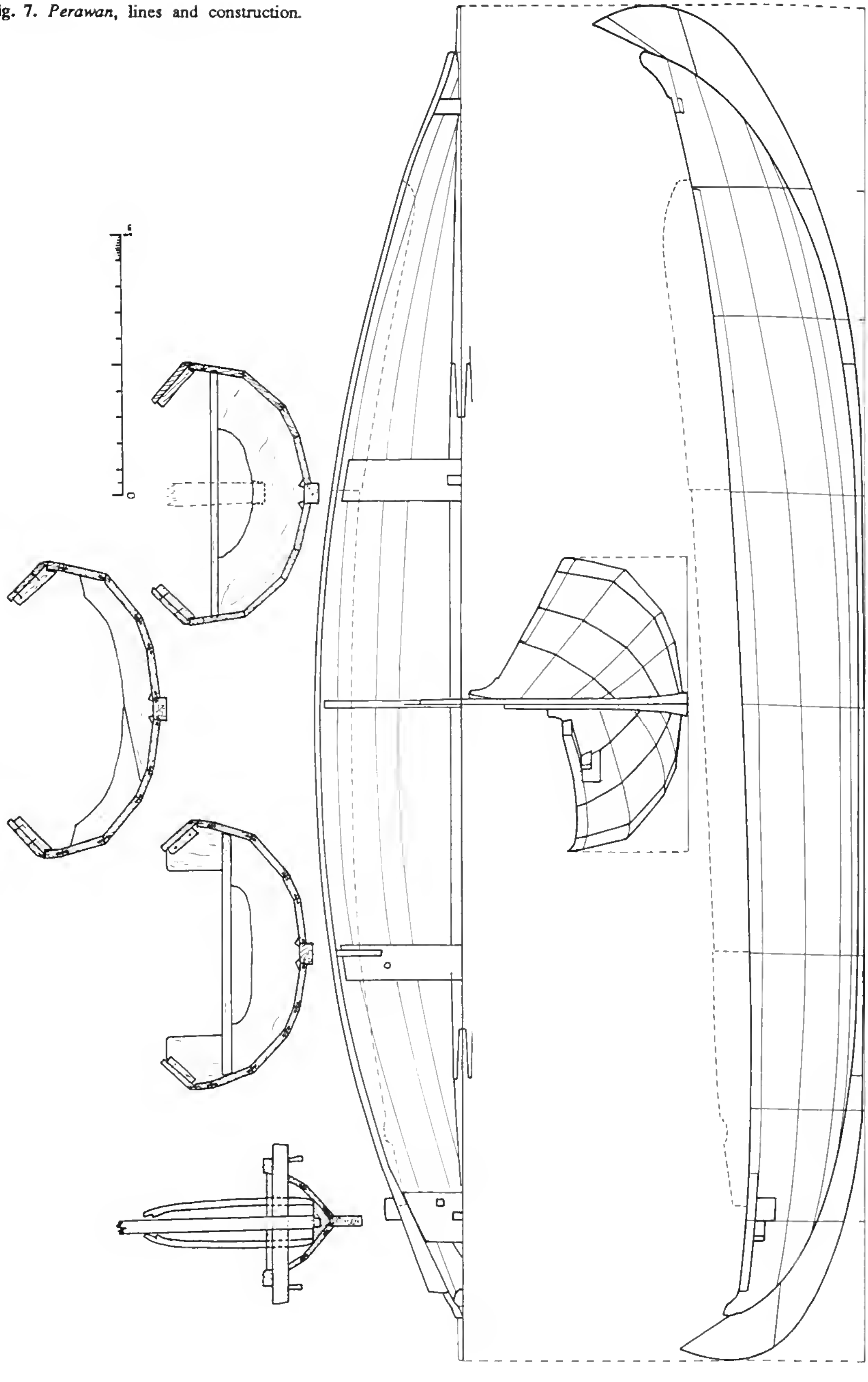


Fig. 8. *Perahu jegongan.*

bon. They carry the same three spritsail rig. Most *seroto* are the size of the smallest *kompreng* (about 5-6m) but a few larger derelict *seroto* could still be seen on the banks of the river west of Cirebon in March 1989. The *seroto* have a stem and stern post but the planking is not always fastened to a rabbett on the stem or stern post. The structure is rather like the simple built-up dugout where the stem butts on to the ends of the planking. There are presumably dowels securing the plank ends to the stem. There is an apron in the *seroto*. The high prow and stern finial are formed partly by the stem or stern post and partly by converging planking. It looks much like a stemless structure. Hawkins (1982:98) shows a *seroto* stern.

The *Perahu Pencoan*. of Waru, East Java has bow and stern profile similar to the *seroto*, although the structure is slightly different (Fig. 22). Waru is a large coastal village about 15km east of Brondong in the *kabupaten* of Lamongan. The *perahu penco* or *pencoan* built at Waru are found in many places along the Java coast at least as far west as Tegal and often they are called *perahu waruan*. They are built with the ends of the planking fastened to a broad stem that projects very little (or occasionally not at all) forward of the planking. Formerly there were large cargo carrying *pencoan* rigged and decorated like Madurese *Golekan* (Fig. 23; Horridge 1981:42-43). Some small *pencoan* have a four-straik form and structure but the majority do not. In some cases the keel projects slightly at the bow and stem.

Small *Perahu* of Central Java. There are, few if any, large traditional vessels built in Central Java. Large *mayang* type *perahu* are purchased from West Java and East Java,

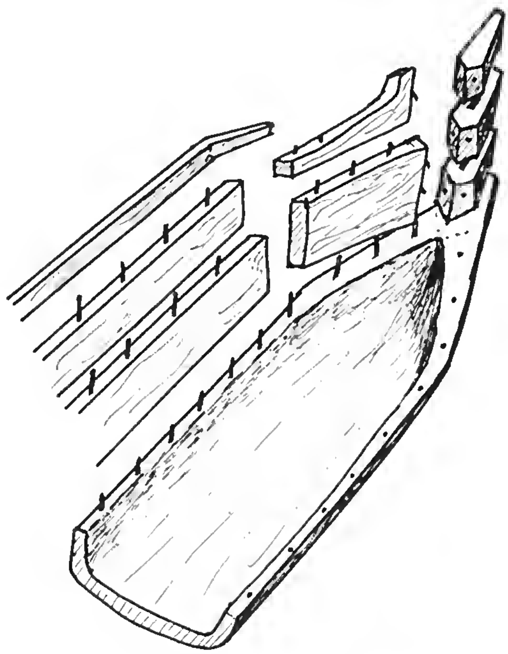


Fig. 9. Structure of Central Java built-up dugout canoe.

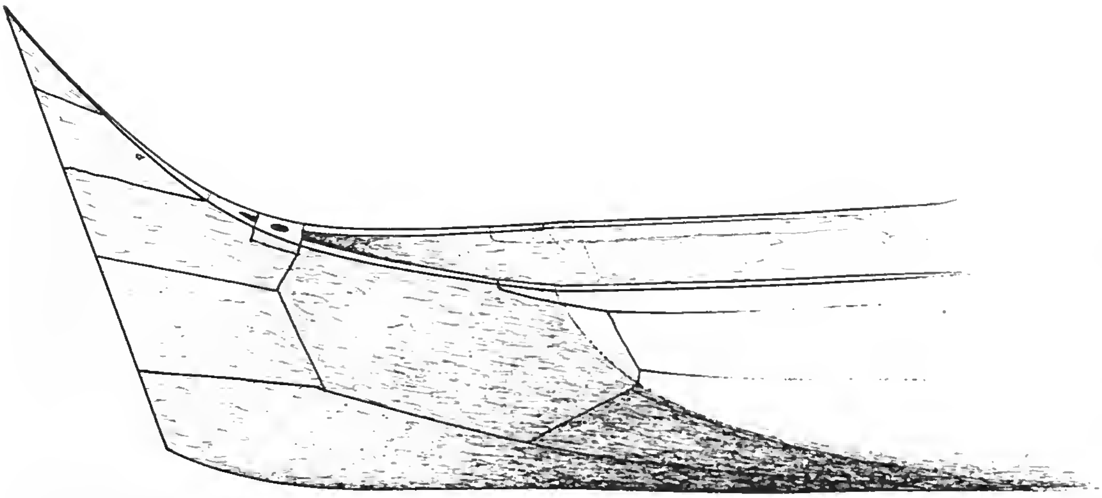


Fig. 10. Bow of East Java *jalan*.

especially from Brondong and Blimbing. There are slightly smaller plain double-ended vessels built in Central Java, some with *may-ang* midsection. These are called *kolek* or *sopek*, or known by more particular local names such as *perahu pekem* and *coklet*, which distinguish local variations in prow style or in hull form.

Perahu sopek of the large promontory between Semarang and Juwana have a distinctive style. There is considerable range of size: small *sopek* are lightly constructed and have little beam. The *sekoci* from Trengganu Malaysia are very similar in shape and structure. The lines of a small *sekoci* brought to Darwin in 1978 as a yacht's tender are presented in Figure 24. The *sekoci* is a type which has been replacing the more traditional and elaborately decorated fishing *perahu* on the East coast of Malaysia since world war II (Gibson-Hill 1954:149). It was presumably introduced from Indonesia since the name is an Indonesian corruption of the Dutch *schuitje* (Gibson-Hill 1950:132).

The best of the larger *sopek* are robust, well built craft with greater beam and a clear four-straik structure. Most of these *sopek* are constructed with a rabbett on the stem and stern-post and with aprons fitted in both bow and stern. On the larger vessels the top of the apron projects above the line of the sheer and forms a small finial (Fig. 25). Similar finials are found on many Javanese *perahu* built further east and there are similar finials on the stemless *perahu jegongan*.

The *perahu pekem* (Fig. 26) is built in the same area as the above mentioned *sopek*, around Jepara. It has a deep and beamy hull and a different structure. The keel is small and hardly projects below the garboard straiks; it is little more than a plank midships. The planks meet in the ends and they are fastened

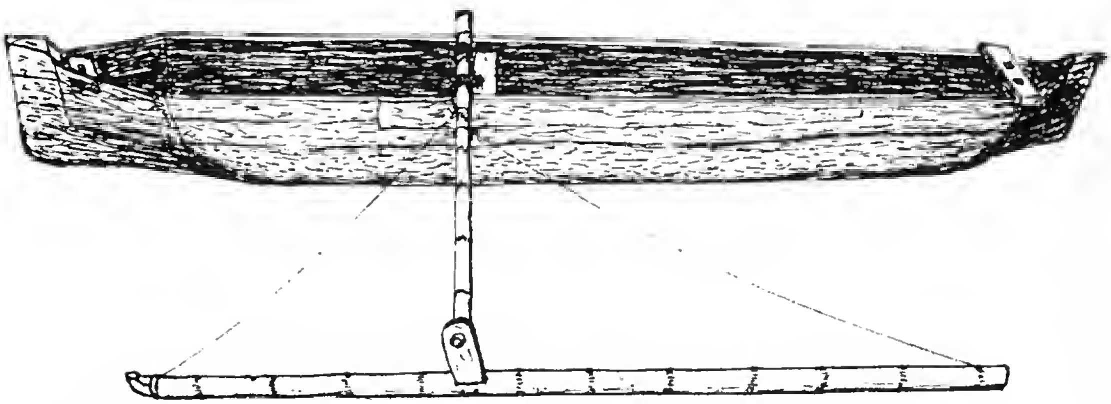


Fig. 11. Outrigger of Central Java canoe

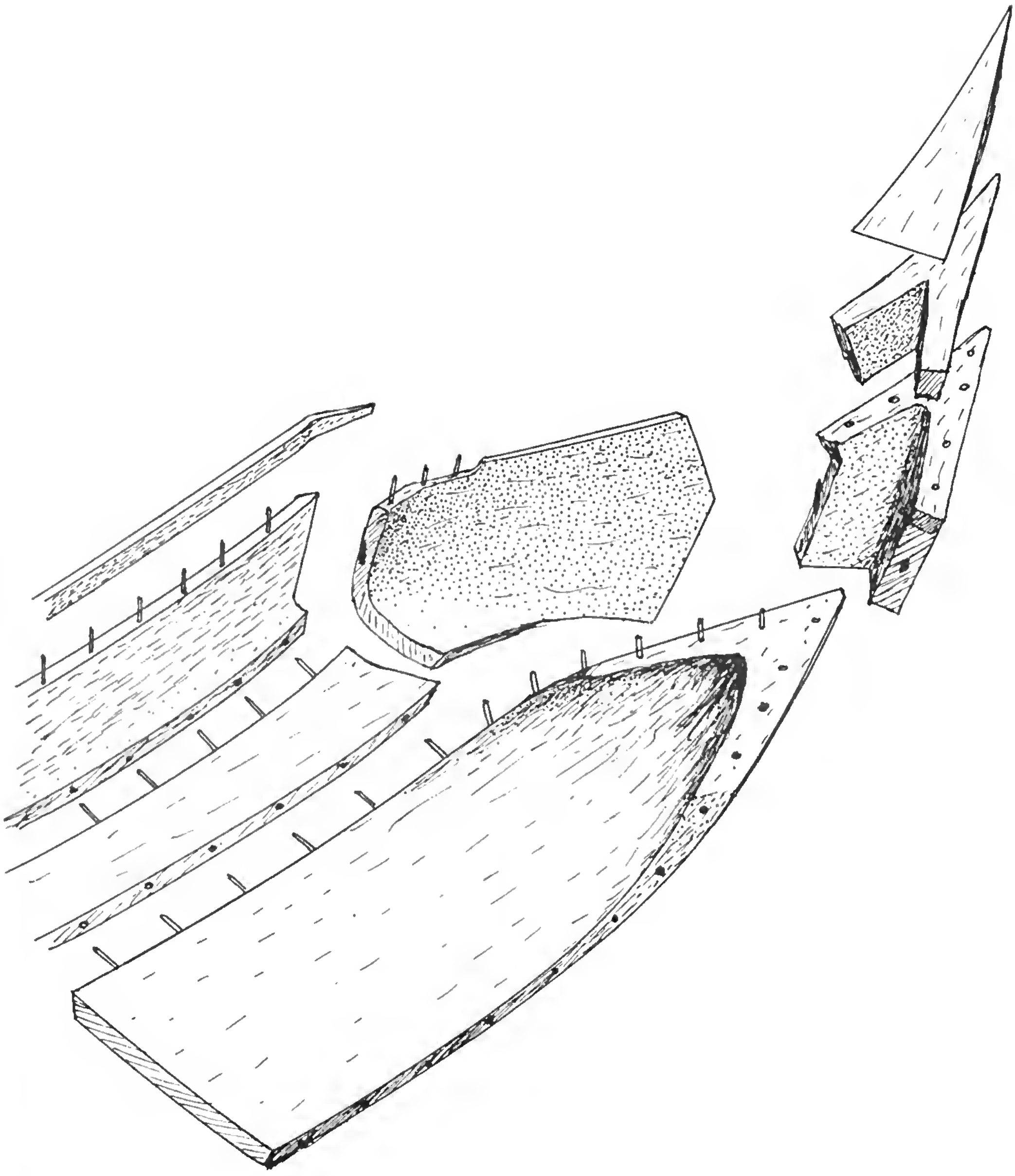


Fig. 12. Structure of East Java *jatan* bow.

to an apron, there is a stem but the plank-ends simply butt on to the aft face of the stem. On a derelict *pekem* at Jepara I could find no fastening of the planks to the stem, but the stem was fastened to the apron. Formerly large *pekem* were used as cargo carrying boats according to an informant at Jepara.

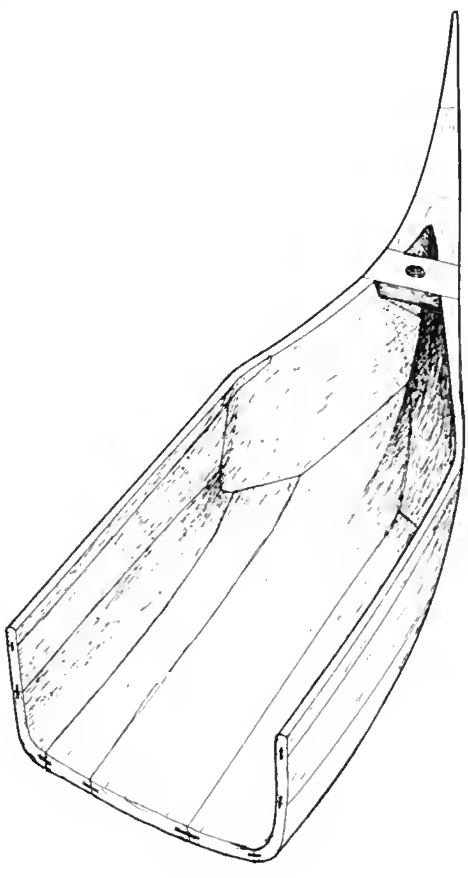
***Perahus* of Brondong and Blimbing.** Many of the *mayang* type vessels found on the Java coast were built in the twin villages of Brondong and Blimbing in the *kabupaten* of Lamongan in East Java. The two main types built at Blimbing/Brondong are usually called *konteng* and *jong* or *ijon* by the people there, but they are often given other names when they are owned and operated elsewhere. For instance, *Terima Kasih* (Figs 1-6) was built as a *konteng* at Blimbing but she was a *perahu beranjang* at Jepara where she was owned. A large fleet of Blimbing-built *jong* operated from Rembang are apparently called *Konting*

there (Horridge 1986:13; Hawkins 1982:104-5).

Both *konteng* and *jong* have four-straik construction. *Konteng* are larger: *Terima Kasih's* dimensions are typical: 11.675 x 3.650 x 1.150m. Nearly all *konteng* are built this size. Scaled down versions are sometimes built to order.

Terima Kasih, now in the collection of the Northern Territory Museum, is a *konteng* which was taken to Jepara, Central Java and fitted with *anjang* fishing gear which made her a *perahu beranjang*. *Anjang* are two long booms which can be rigged out to port to spread a net horizontally in the water. At night pressure kerosene lamps suspended over the net attract fish and squid which are caught when the net is winched up. *Beranjang* operate out of Jepara especially around Karimun Jawa islands. The same fishing technique is used in other areas with nets spread from stationary platforms (*bagan*), large outriggers (*bagan satu*) and large catamarans (*bagan dua*). *Beranjang* cannot spread such large nets as *bagan* but they are more suitable for making a passage in a seaway.

Fig. 13. East Java *jatan* bow, internal view.



Terima Kasih has a small cabin built on her starboard side leaving the port side clear for handling the nets and *anjang*. *Konteng* at Blimbing usually have no cabin while *konteng* used for cargo carrying have large cabins formed by roofing over most of the hold (Fig. 27). Cargo carrying *konteng* are operated from Sedayu Lawas near Blimbing and were formerly operated from Karimun Jawa.

The construction of *Terima Kasih* provides a good example of *mayang* type construction. The *konteng* of Blimbing are built to a formula, there are no plans or written table of dimensions but the size of each of the four straiks is fixed. A full size *konteng* has thirteen frames, whereas a full size *jong* has ten frames. In *Terima Kasih* ten of the frames are constructed as bulkheads. Forward there are two heavy frames which almost form bulkheads and aft there is one smaller grown frame. *Konteng* under construction at Blimbing in March 1989 all had thirteen bulkheads. These bulkheads are not built-up to the level of the rail. At about the level of the third chine the bulkheads support large thwarts. Top futtocks or top pieces (*toplet* or *taju*) set into the bulkheads project through the thwarts and support the fourth straik. They do not support the heavy rail timbers (*golak* or *gotek*) which are edge-dowelled on to cap the planking. Above the *golak* there is a low wash straik.

All the planks are edge-dowelled together with 12mm diameter dowels set at 75mm centres, they are all locked by locking pins. In recent years this practice has changed: now four of every five dowels are replaced by mild steel pins. The dowels are usually *kayu pung* (*Dichrostachys cinerea*). The planking and all other timbers are teak (*Tectona grandis*). The four straiks are very wide; the third straik is 720mm wide and only 25mm thick at the midsection. Such wide planks would be very likely to start (loosen) the caulking or luting and break the edge-dowels by expanding and contracting if they were not high quality teak, which expands and contracts very little in response to changes in ambient moisture.

The planks are long but do not run the full length of straiks. The butts are tapered (diagonal to the run of the straiks), and they are arranged to lie where there is most curve or twist in the straiks so that the need to bend

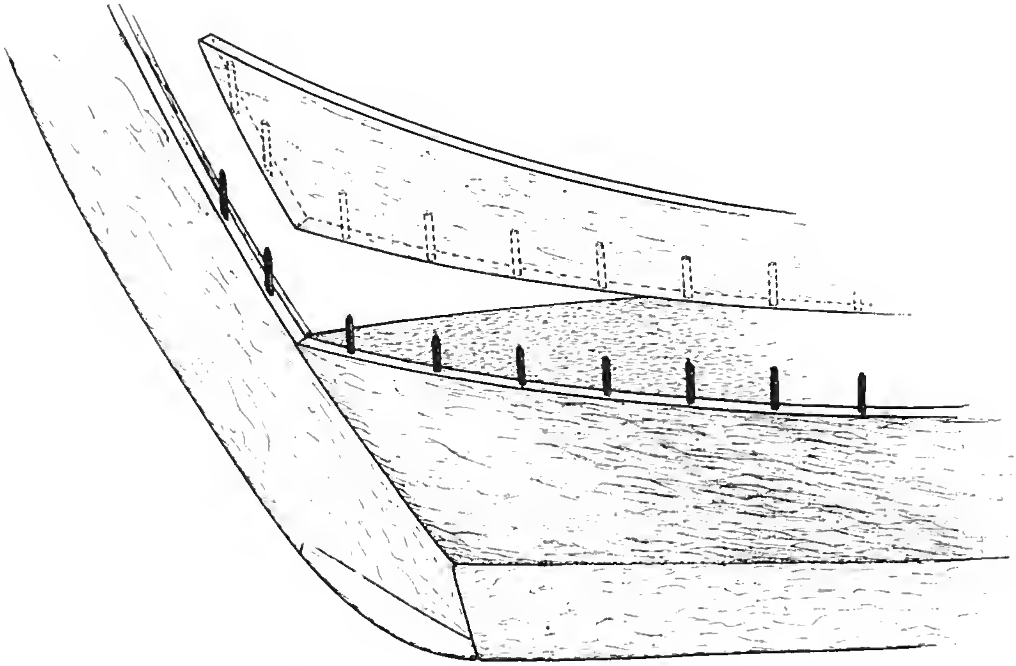


Fig. 14. Edge-dowelled plank fastened to aft face of the stem by dowels.

planks is minimised. The run of the straiks and position of the butts is indicated on the sheer plan (Figs 1, 3).

There is no rabbett on the stem. The forward ends of the planks meet where they butt onto the aft face of the stem; the plank ends are dowelled to the stem (Fig. 14). The stem is also secured to an apron but this apron was fitted at Jepara by Central Javanese boat builders. Aprons are unknown in *perahu konteng* at Blimbing.

The keel is two lengths of timber searfed midships, however in many *konteng* the keel is a single timber, and in recently built vessels it is a much more substantial timber. There are keel bolts fastening the bulkheads and frames to the keel. The bulkheads show a variety of structures, some are frames eomposed of floors and top pieces with lighter planking fitted to eomplete the bulkhead to the level of the thwart. Others are eomposed of heavy timbers layered horizontally. The structure of seleeted bulkheads is indieated on the construction plan (Fig. 2).

The mast is stepped through a large thwart into a large thwartship mast step timber, which is a floor fitted immediately abaft of the bulkhead. The mast heel is tapered so that it wedges into the aperture in the step and does not touch the keel. The only standing rigging is a single baekstay leading well aft so there is little downward force on the mast.

The two thwarts *(dapuran)* in the stern which step the rudder mounting post and the large boom crûtch are let through the hull planking. They project slightly like the rudder mounting beams *(sangkilang)* of traditional South Sulawesi *perahu* (cf. Horridge 1979: Fig. 18) but the rudder is not secured against these beams so the projection is funetionally redundant. The erutch which is stepped through the *dapuran* would take considerable load when bearing the weight of the spars, sails and drying nets if the vessel was rolling. It has been suggested that the crutch also supports the mast through a "bar" (*andang*) connecting the mast to the crutch (Horridge 1981:47). This is the not the case on *Terima Kasih* nor is the *andang* strong enough to effectively stay the mast on any *mayang* that I have had the opportunity to inspeet.

The rudder mounting system (Fig. 6) is typical for Javanese vessels. The enormous rudder is always carried on the lee side and must be shifted around the stern when the vessel wears on to the other tack. The loom or stock of the rudder is heavy enough to eounterbalance the blade of the rudder so that the rudder ean also be used as an oar if the head of the stoek is unshipped from the mounting post.

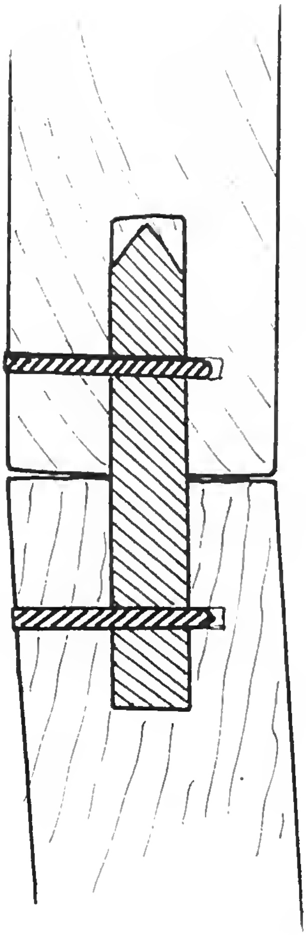


Fig. 15. Section through edge-dowelled planking showing locking pins.

There is no fixed deck but there are permanent fore and aft timbers between the thwarts along the centre line. These are fitted on most *mayang* type vessels. At Blimbing they are called *sendeng* while at Indramayu they are *sentang*. No bilge pump was fitted on *Terima Kasih*. Water was removed from the bilge by bailing. The planking in the bilge has been abraded by bailing to such an extent that the edge-dowels between the planks have been exposed in places.

The rig (Fig. 5) with the large quadrilateral sail was once standard on *perahu konteng*. It is still used at Jepara (pers. obs. March 1989) but in East Java the *lete* rig (Fig. 29) is now standard. The upper spar is built of laminations and battens of teak held together by thousands of siezings of monofilament nylon fishing line. The spar is formed with the aft end very tapered and curved.

Terima Kasih was purchased at Jepara by Jamie Munro and the late Jerry Williams in 1982. They sailed her to Darwin with no other crew. She was at that time fairly old and leaked, especially around the forefoot where some fastenings and dowels had failed.

At Darwin she was sailed in company with some Indonesian *perahu lambo* which are sailed there as yachts. She was not as fast, nor as weatherly as the *lambo* in spite of her fairly generous sail plan.

Perahu Jong* or *Ijon of Blimbing (Fig. 28; Hawkins 1982:104-5) are smaller and slightly less heavily built than the *konteng*. At full size they are 9 x 3.3 x 1.15m, the lines are similar but tend to be slightly fuller. They are very popular fishing boats and can be found in many places along the Java coast, known by various local names such as *ganibu* and *coklet*, but they always originate from Blimbing.

The structure is similar to that of the *konteng*; the planking meets at the ends and is edge-dowelled to the inboard faces of the stem and stern post. Immediately aft of the prow there is a second prow finial formed by the conjoined ends of the rail and an apron-like piece (Fig. 25). This is similar to the structure noted on the Central Java *sopek* but in the case of the *jong* the apron piece is short. It does not extend below the fourth straik.

In the bow and stern there are thwarts dovetailed into the rail which help tie the ends together. It is the practice of the builders to set up turnbuckles or a spanish windlass to pull the ends together while fitting these thwarts.

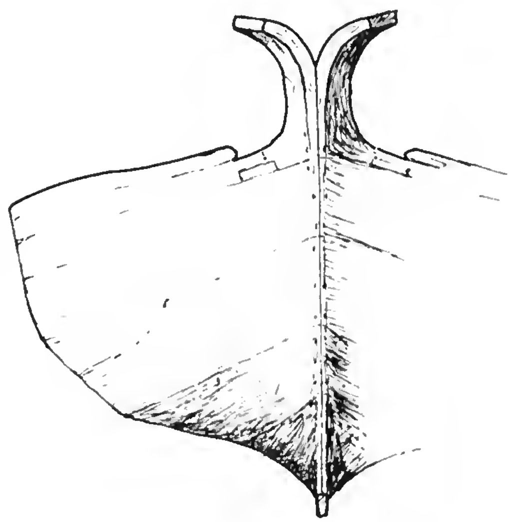


Fig. 16. Prow of a *perahu condong*, West Java.

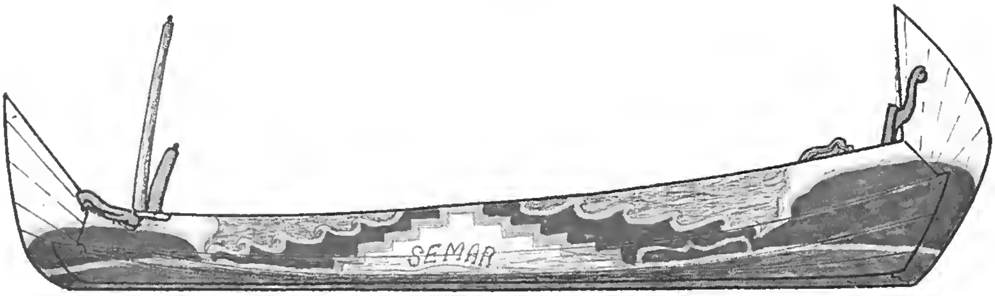


Fig. 17. Profile of a *perahu compreng*, West Java.

The thwart in the stern is called *cengkal kemi* (*kemi* or *gemi* can mean stern and can also mean join or splice in nautical vocabularies of Indonesia).

Like *konteng* the *jong* are built entirely from good quality teak. Virtually all large *jong* are now fitted with small "long shaft" diesel motors which can be used for propulsion and to drive winches for handling nets. They also carry *lete* sails. Most *koteng* and *jong* have exuberantly colourful paint work which is executed in the yards where they are built.

Perawan*, a small *pedetan, is a vessel in the collections of the Northern Territory Museum. She is a very small example of a type that can be called *pedetan*, *bedetan* or *golekan* from Pasuruan in East Java

She was sailed to Australia in 1981 by a lone Dutchman, Thomas Johannes Meynen who died shortly after making an unfortunate landfall on uninhabited Grosse Island (12°35'S, 130°25'E). *Perawan* was later recovered by Northern Territory Museum staff, although some of her gear, including the rudder was missing. Double outriggers were fitted but they appeared to have been added for the voyage to Australia. They were very crudely fitted and showed signs of previously being fitted to a different type of vessel. The style of outrigger booms that were fitted to this vessel are found fitted to canoes at Pasir Putih in East Java (Horridge 1987:Fig. 7a) which are built at Pasisir near Besuki.

The midsection shows the four-straik construction (Fig. 7). There is one frame and two bulkheads which support thwarts. Aft there is a small bulkhead which has little structural significance because there are virtually no fastenings holding it in place. The keel is wide and shallow, midships it hardly projects below the garboard straik and it is made up of three pieces. The middle section is straight, the end pieces curve upwards and become narrower and deeper towards the ends. These pieces are scarfed on to the middle piece with long tenons (see Horridge 1979:12, 1987:73 for discussion of the symbolic significance of this type of structure). The stem and stern post are

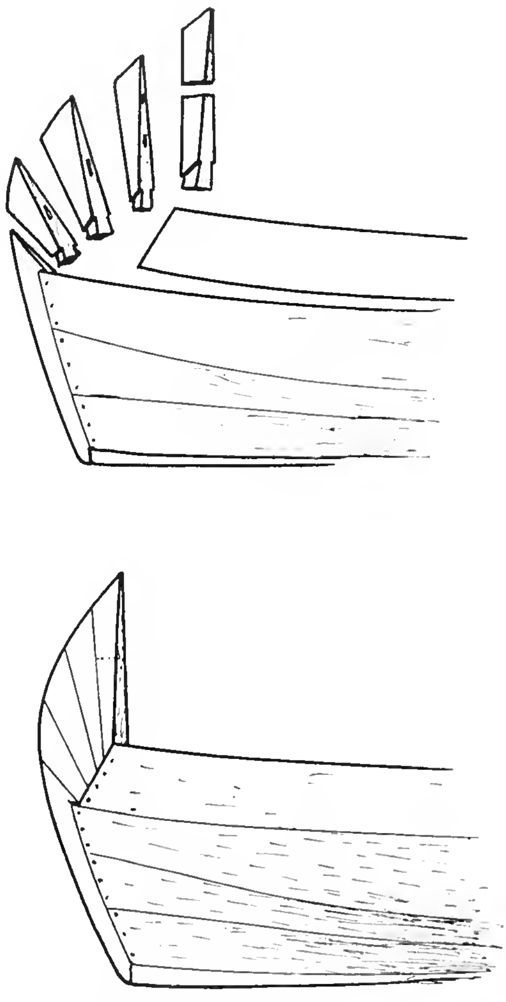


Fig. 18. Structure of a *perahu compreng* bow.

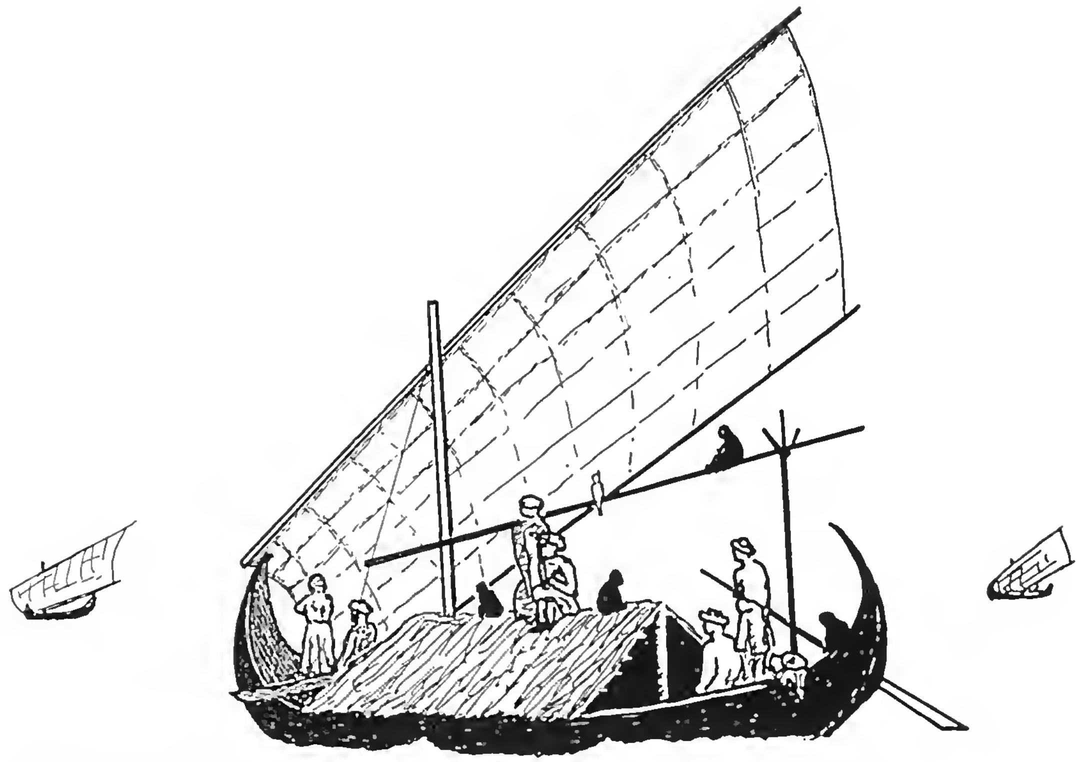


Fig. 19. *Perahu mayang*, circa 1830, redrawn by the author from a contemporary engraving by E. Duncan. There appears to be no stem or sternpost.

fitted onto the upper face of the keel extensions (Fig 7). There is no rabbett and no fastening of the top straik to the stem. The stem and stern post are effectively only decorative finials on the projecting upswept ends of the keel. The upper planking is held together in the bow by a thwart and in the stern by the short apron-like structure described on the *perahu jong*.

Perawan is built of teak with mangrove (*Rhizophora* sp.) dowels. The edge-dowels are fitted with locking pins. The planks are fastened to the three frames with mild steel nails, most of which have rusted away. She had no leaking seams when she was recovered.

Semanis*, a small *lete is from the Madurese tradition (Fig. 29). *Semanis* is a fishing vessel from Muncar, East Java, now in the collection of the Northern Territory Museum. Although she was owned and operated from Muncar she was probably built on one of the Kangean islands east of Madura, or by builders from one of the islands east of Madura. On her registration papers she is described as a *golekan*. Another *perahu* of the same type from Kangean, now in Darwin, is described on her papers as "*Mayang Model Lete*", which indicates a fishing vessel built in the *lete* style. *Lete* is the standard spelling of the name sometimes spelt *leti* (Horridge 1981, 1986; Hawkins 1982) and *leteh* (Gibson-Hill 1950).

Semanis does not have four-straik structure or form, nor does she have bulkheads. There are six straiks forming a rounded bilge. There are thirteen frames, two are close together and bear the mast step. All the frames include floors. There are no half-frames. Some frames consist of single large timbers extending from rail to rail. Other frames include top futtocks fitted on one or both sides. Not all these top futtocks are original, some were fitted to replace rotted ends of the original grown timbers by Mr Jamie Munro when he purchased *Semanis* in 1979.

The planking is capped by a solid rail much like that on a *konteng* but it differs in that it is supported by the frames. Above the rail there are high wash straiks. These wash straiks were originally single planks of teak from bow to stern edge-dowelled to the rail. They contributed significantly to longitudinal strength. When they became rotted in Darwin *Semanis* became badly hogged (the bow and stern sagged). She has now been restored.

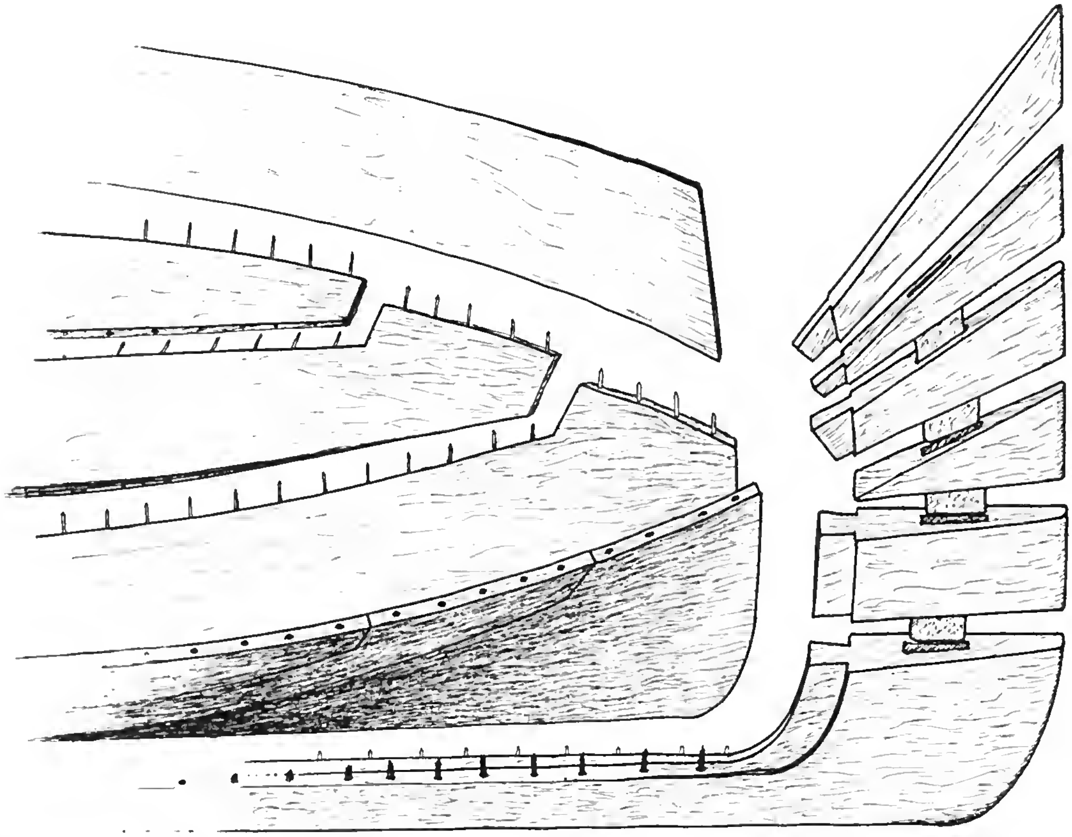


Fig. 20. Structure of *perahu compreng* stern.

The rails turn upwards to form large finials where they meet at the bow and stern. A short apron-like piece is fitted between the convergent rails and the assembly is fastened together with dowels. This structure holds together the upper straiks which are not fastened to the stem. The upper part of the stem is a separate block dowelled onto the stem; its function is decorative.

This structure is standard for *perahu golekan* and *lete lete*. On the *perahu golekan* the rail finial structures are large while on modern *lete* they are small or even vestigial (see Horridge 1981: Pl. E, G, H, J, K). The *golekan* intended here is the vessel identified in Horridge (1981) but not the *golekan* in Hawkins (1982:64-66), which are more often called *kroman* or *janggolan*.

The mast on *Semanis* is stepped through a large thwart and wedged into the mast step in the same way as described for *Terima Kasih* but the mast step is supported by two floors rather than sitting on the planking. The thwart is supported by stringers rather than a bulkhead.

The rudder is carried on the leeside as on the *mayang* but it is fitted into a notch on the aft side of the large thwart mounted on the stern. In this respect the rudder mounting is similar to the double rudder mounting system on traditional Sulawesi *perahu*. Javanese *perahu* (with the exception of the large cargo carriers of Sedayu Lawas) carry the rudder against the rail well aft of the major thwart in the stern. Madurese *golekan* and some other types carry their rudder lashed against the rail and the aft side of the thwart.

Semanis carried *lete* rig. She was sailed to Darwin in 1979 by Jamie and Michael Munro. Another similar and slightly smaller *perahu* from Kangean was sailed to Darwin more recently by Peter Walker and is still used as a yacht. She has proved faster and slightly more weatherly than the *perahu lambo* in Darwin. Her hull is very shallow but the large rudder confers adequate resistance to leeway and the *lete* rig is powerful.

Madurese perahu lis alis. These distinctive Madurese craft range in size from canoe size upwards. Larger sea-going, cargo-carrying

Fig. 21. Stern of *perahu compreng* under construction, the planking is in place and the aft frame or apron has been fitted but the sternpost is not yet fitted.

versions are called *kroman* and *janggolan* (Horridge 1981:32-34). They are distinguished by narrow transoms in the bow and stern and projecting ends of the keel (Fig. 30). In small *lis alis* the keel structure is similar to that in *Perawan*. The middle section of the keel is only a central plank; the size and shape of the projecting up-curving keel-ends suggest that there is a sturdy keel projecting below the hull, but this is not the case. The bottom of the transom is lightly tenoned into the keel-ends but it is held in place mainly by the planking which is fastened to it. Small *lis alis* often have four straiks but they are narrow and do not have the midsection of a *mayang*. They are similar to the *pencoan* in form and structure. There are few, if any ribs fitted in small *lis alis*, there are thwarts which stiffen the hull. Some of these thwarts are let through the planking.

DISCUSSION

The four-straik structure and hull form is found all along the Java coast where it is a strong prevalent tradition. Perhaps four-straik construction was more recently introduced to Madura where most *perahu* have a rounded turn to the bilge.

The four-straik structure imposes an upper size limit: to build a four-straik vessel substantially larger than a full-size *perahu konteng* would require planks of exceptional width. The design might derive from a sewn plank small boat tradition. There is a Southeast Asian sewn plank tradition which has an ingenious but very laborious system of sewing the planks together with stitches that are not visible on the outside of the plank seams (Manguin 1984). In the context of this particularly laborious technique there would be an obvious advantage in having only four straiks and therefore only four seams to stitch on each side of the hull. The reliance on the locked edge-dowels to hold the hull together, almost without frames as seen in small boats like *Perawan*, suggests a structural affinity with sewn plank canoes.

Sewn plank boats called *Masula*, which are built with four straiks, exist in Southern India (D. Dwyer pers. comm.). These vessels might be part of a related tradition although the sewing technique and the hull form are not the same as those of Southeast Asia.

The very large Javanese vessels of several hundred tons burthen encountered by early European navigators in Southeast Asian wa-

Fig. 22. *Perahu pencoan* from Waru, East Java.

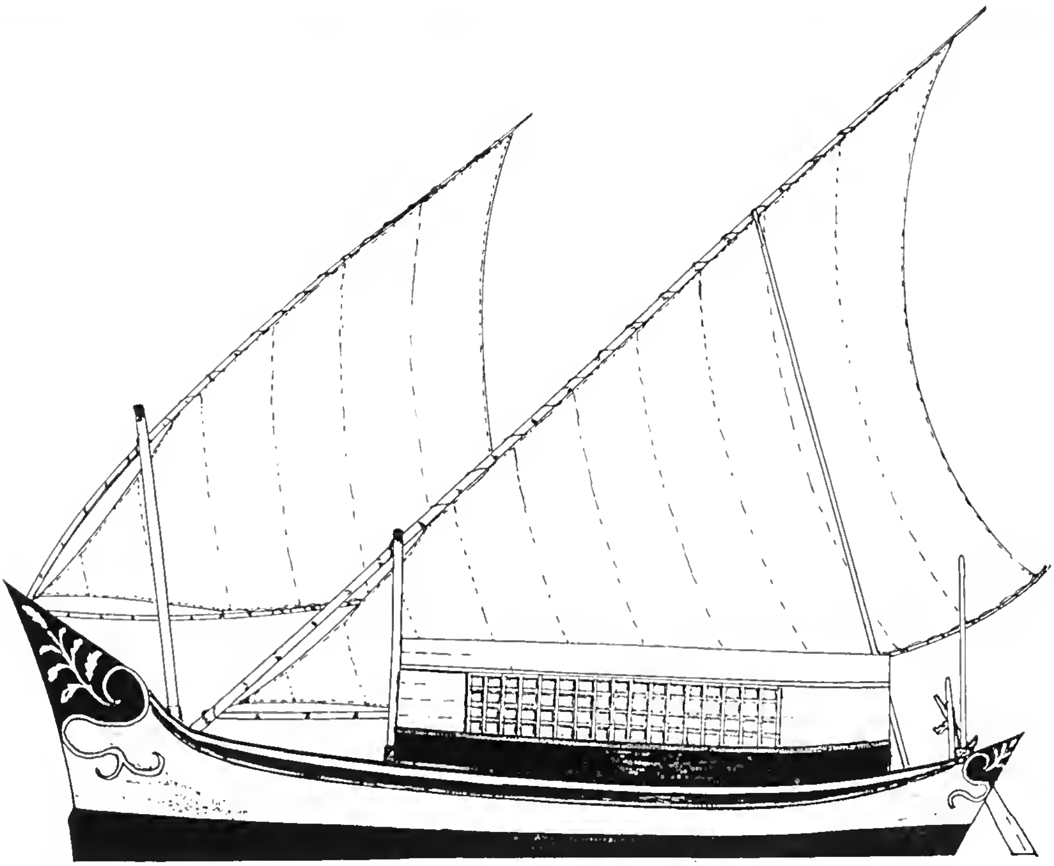


Fig. 23. Sketch of a large *perahu pencoan.*

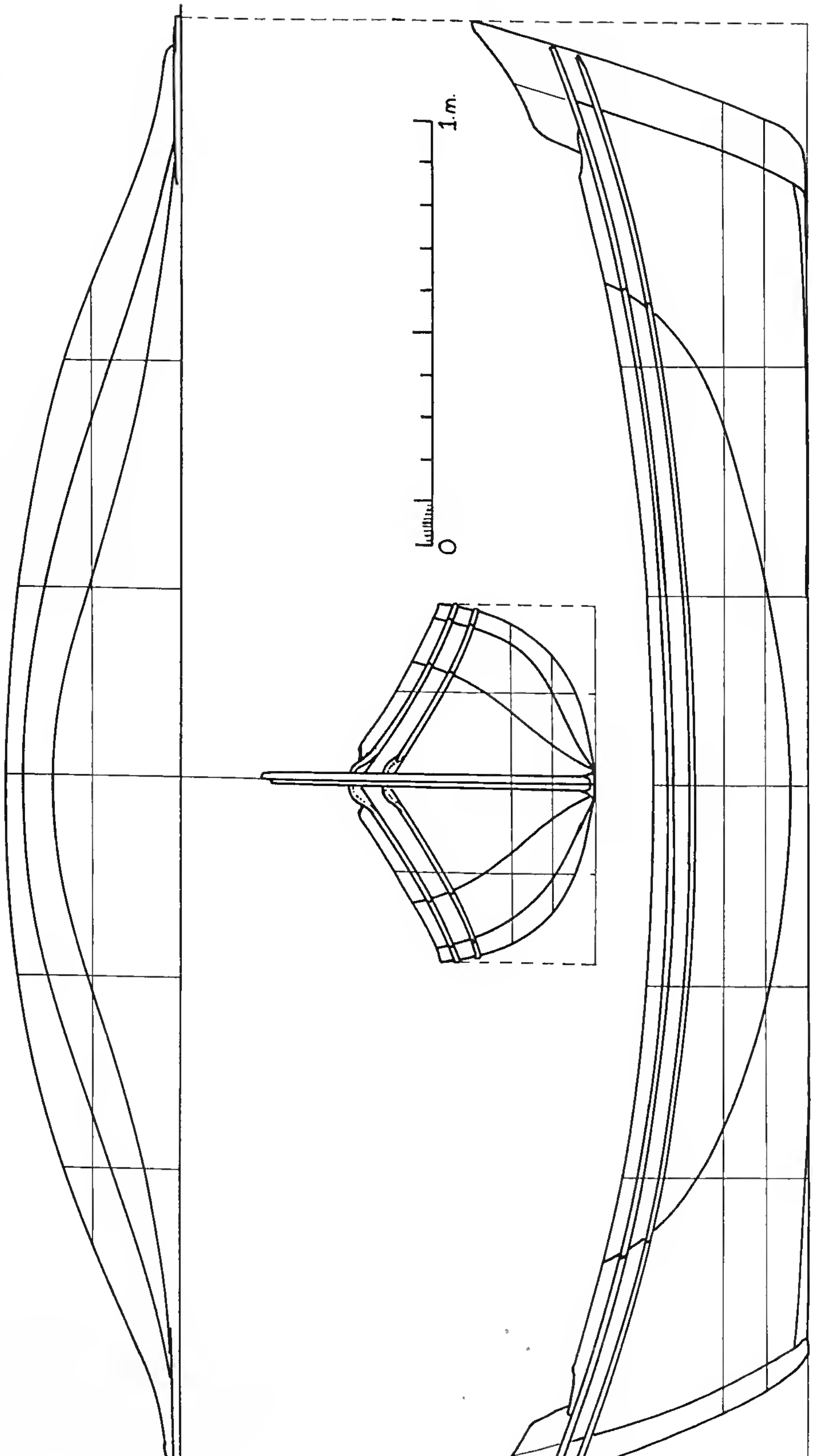


Fig. 24. Lines of a *sekoci* from Trengganu, Malaysia. The small *sekoci* is constructed with four straiks, the stem and stempost are fitted onto the ends of the planking and the keel does not project below the planking.

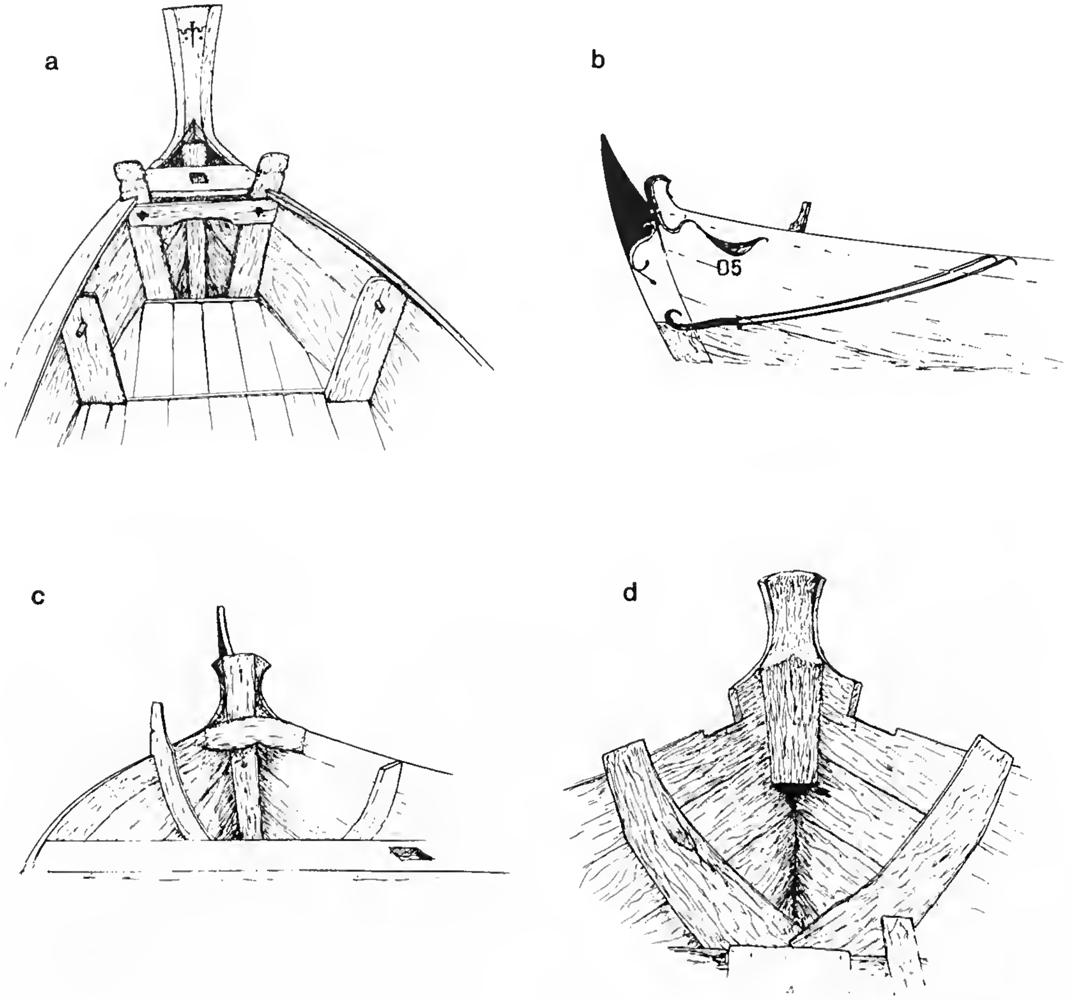


Fig. 25. a. Bow of a stemless *jegongan* showing forward frame, apron, forward thwart and prow finial with separate apron piece. **b.** Bow of large *sopek* from Central Java. **c.** Internal view of *sopek* bow showing the apron extended into the bow finial. **d.** Internal view of a *perahu ijon* bow showing the short apron piece extended into the bow finial.

ters, called *Jong* or *Jonque*, could not have had a four-straik structure (Manguin 1980). The *mayang's* construction and form were presumably archaic when the first Portugeuse vessel sailed into Southeast Asian waters. This conforms with Bowen's observation (1952:186) that "The sum total of the evidence in the Indian Ocean shows that fisherfolk cling most tenaciously to primitive forms of watercraft. Mariners, on the other hand, usually sail in craft that have been strongly influenced by foreign elements".

The rudder mounting system seen on Javanese *perahus* seems to be a design for small craft. It is a system which allows the rudder to be quickly unstropped and used as an oar although the rudder of a *perahu konteng* is too large to be easily handled in this way. Large Javanese *perahu* have almost disappeared, and the few that operate from Sedayu Lawas in East Java have a quite different rudder mounting system, even though some of the Sedayu Lawas *perahu* are actually large *konteng* planked up to more than twice their original moulded depth.

A standard *perahu konteng* such as *Terima Kasih* has two slightly projecting thwarts or beams in the stern which could be interpreted as vestigial quarter-rudder mounting beams. Another Javanese cargo carrying *perahu*, the *perahu kacik* of East Java (Horridge 1985:Pl. 2) also had (or have if any still exist) two

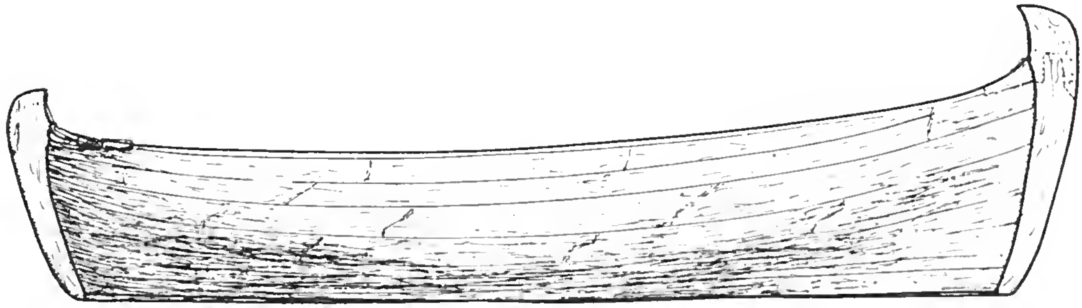


Fig. 26. Sketch profile of *perahu pekem*, Central Java.

Fig. 27. Cargo carrying *perahu konteng*, Sedayu Lawas, East Java.

projecting beams in the stern which could be interpreted as vestigial quarter-rudder mounting beams. They had no obvious function, but greatly resembled the rudder mounting beams of large Sulawesi *perahu*, except that the lower beam was slightly forward of the upper one on a *perahu kacik* whereas the lower beam is slightly aft of the upper one on a Sulawesi *perahu*. If quarter-rudders were mounted on beams positioned like those of a *perahu kacik* they would be secured against the aft side of the lower beam and the forward side of the upper beam (unlike the Sulawesi system which has the rudder against the aft side of both beams). Such a system might be more convenient with the long projecting rudder stock of the Javanese rudder.

The use of bulkheads rather than ribs is a feature of ancient Southeast Asian ships. Furthermore, the bulkheads were luted as if to make them watertight but had limbers to allow the passage of water in the bilge in ancient boat building (Green and Intakosai 1983:8), as in modern Javanese *mayang*. The number of bulkheads was most frequently twelve on the evidence of hulls discovered by maritime archaeology (Green and Harper 1987:2-4). In Indonesian boat building there is also a tradition of twelve frames, corresponding to the ribs of a human (Horridge 1979:13, 1981:57). The use of thirteen bulkheads in all *perahu konteng* and some other large *mayang*, and also the thirteen frames in *Semanis* seems to be a different tradition. Perhaps this reflects

Fig. 28. *Perahu ijon* from Blimbing, East Java.

Javanese preference for odd numbers which they believe to have magical powers.

The bow and stern structures vary regionally. There are completely stemless structures although most types have a stem timber. In most cases the stem does not have the same structural function as in western boat building, because the hood ends of the planks are not fitted into a rabbett on the sides of the stem. In some designs, especially of those of East Java and Madura, the ends of the keel turn upwards and the lower straik or straiks run out on the upturned keel ends, so these upturned ends function as a lower stem and stern post. On the *perahu lete* and similar types a complete stem sweeps up from the keel, but there is always a stemless structure for the upper straik or straiks, and the upper stem is mainly decorative. On *perahus* such as the *konteng* there is a full stem fitted on to the end of a straight keel, but the plank ends are edge-dowelled to the stem as they are to the upturned keel in other designs. In virtually all cases thwarts help tie together the two sides of the vessel in the ends. The stemless upper structures generally include an apron-like piece, but this is not identical to the apron in traditional western boat-building. The full length apron found in some Javanese *sopek* and the Trengganu *sekoci* (called *serang* in both places) could be an adaptation of a traditional structure and not entirely a copy of western boat-building.

Early European representations of Javanese *perahus* seem to show stemless vessels with profiles like that of the *kompreng*. Examples include a 1598 engraving in *D'Eerst Boeck* (reproduced in Manguin 1980:271), drawings by Sidney Parkinson, 1771 (reproduced in Joppien and Smith 1985:232, and redrawn in Horridge 1981:47), and most clear is a *mayang* in the foreground of an engraving by E. Duncan, from a W.J. Huggins painting of the ship *Sir David Scott* entering Sunda Strait February 1830 (redrawn here in Fig. 21).

The structure with the lower planking running out on a keel/lower stem but no upper stem could have been a feature of the larger merchant *jonques* of pre-colonial Southeast Asia.

A curious design affinity exists with some archaic *dhows*. Some of the sewn plank *dau* of Lamu, north of Zanzibar were apparently stemless above the first straik (McGrail 1981: Pl. 31; Hornell 1941:Fig. 1a) and the *zarouk* of southern Arabia had a very raked stem and stern post which terminated just above the load water-line (Hawkins 1977:74). There are also smaller boats of sewn plank construction in south Arabia which are built with chines and have other features in common with

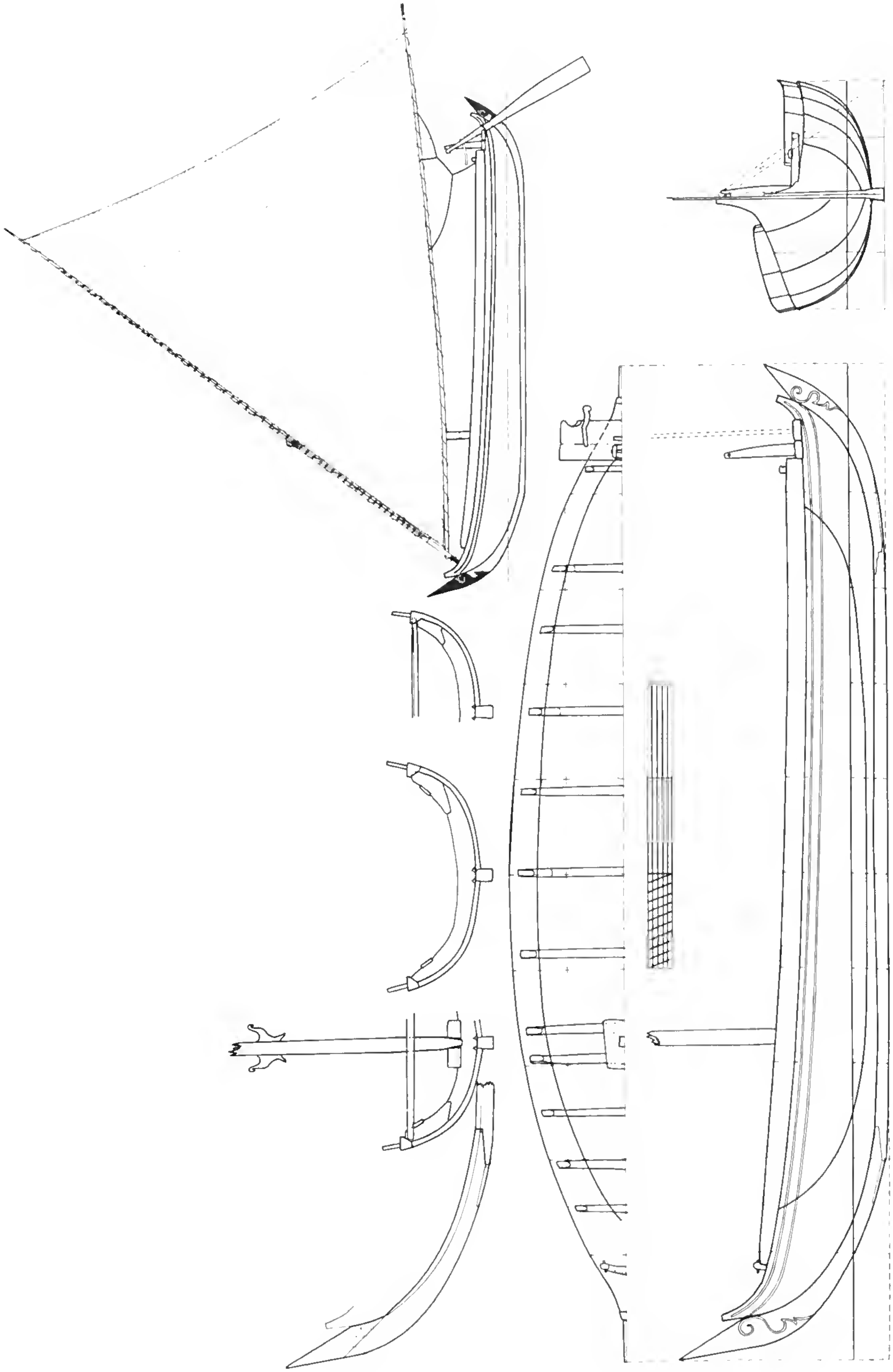


Fig. 29. *Semanis*, lines and construction.

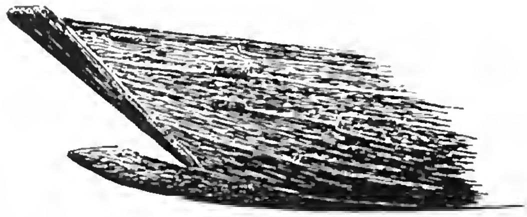


Fig. 30. Bow of a small *lis alis*.

Javanese *perahu*. The stem, keel and sternpost are succinctly described by Bowen (1952:210).

The stem and sternposts are straight members, roughly twice the thickness of the planks, which come together at the bow and stern. The planks are not rabbetted into the stem and sternpost, but simply butted against them. The keel is a flat member which narrows at the bow and stern to the thickness of the stem and sternposts.

This could be a description of a Javanese *perahu* or a Trengganu *sekoci* if slight curve of the stem and sternpost is allowed. The stem butted on to the end of the planks is in fact necessarily a feature of sewn plank construction if any stem is used; it is not possible to sew the plank ends into a rabbett. The stem is therefore of limited structural value; it helps hold the planking together and stiffens it vertically. A stem is not necessary in shell constructed vessels of little depth such as built up dugout or in larger vessels strongly built with thwarts, frames or bulkheads.

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THE FACTORS OF REVOLT

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ABSTRACT

This research essay introduces a frame of reference for the analysis of the Theory and Practice of Communist revolution.

KEYWORDS: Revolution, Communist, Malaya, Theory, Ideology, Leadership, Communist Party of Malaya, Lenin, Factors of Revolt, Causative, Effective.

INTRODUCTION

"Without revolutionary theory there can be no revolutionary movement."

What is to be Done
(Lenin 1988:91)

Politics, when stripped of its abstractions, might be ungraciously described as the competition for and justification of, the exercise of power.

However, in an attempt to apply a degree of order (and presumably dignity) to the world, social theorists have established a veritable bibliotheca of abstractions, theories, typologies and models explaining what politics "really" is.

These divergent theories of society and politics sometimes cloud the issues under examination. The resultant confusion is compounded by interminable disagreements among social theorists about their terms of reference. As John Plamenatz succinctly observed:

> There are sociologists and political scientists who put themselves to great trouble to define the terms they use and to state their assumptions. They do not always do it well. (Plamenatz 1969:XI).

A case in point is the question of revolution.

Theorists of revolution are legion - the 'Great Revolution' school, functionalists, Marxists, Communists, anarchists and nationalists to suggest a few. The volume of their theoretical endeavour is confounded by the confusing litter of revolutions throughout history - the Agrarian and Industrial Revolutions, the Technological and Computer Revolutions, the Green Revolution, the Glorious Revolution, the October and Cultural Revolutions and, in recent vogue, a variety of 'People's Revolutions' - to list a cross section.

Given that revolutions, in all their various guises, have come to dominate twentieth century political history, it is not surprising that the notion of 'revolution' has spawned a formidable body of revolutionary theorists - many of whom would agree with the premise that revolution has become the 'central concept in the vocabulary of modern political thought.' (O'Sullivan 1983:4).

Needless to say, there is no accepted frame of reference about the nature of revolution. Indeed, ethical and social scientific distinctions between revolution, rebellion, insurrection, insurgency, guerrilla war, terrorism, civil war and other manifestations of internal belligerency, abound.

It is not the object of this paper to present yet another general theory of revolution. It is rather, the very limited object of this paper to introduce a frame of reference to analyse a particular aspect of a particular type of revolution.

In so doing, the paper will be predicated upon two premises, namely:

a. in the general historical sense, revolution can be understood as an abrupt, distinctive and determinative process of change distinguishing a given period of history from its predecessor

and

b. in the political sense, revolution can be understood as an extra-legal challenge to power through the application of political violence.

In the case of Malaya, the Communists sought recourse to political violence in their challenge to power. This political violence was subsequently described by the Communists as the 'Malayan Revolutionary War'. (CPM:1948). This essay is a component part of a major study of the Communist movement in both Singapore and Malaysia.

The Communist Party of Malaya (CPM) has consistently claimed its theoretical legitimacy through its adherence to both the Theory and Practice of Marxism-Leninism. *Ergo* it has always seen itself as a revolutionary party and proclaimed its doctrinal purity accordingly. Recurring themes within this doctrine suggested the frame of reference hereafter described.

Significantly, the history of the CPM mirrors one of the fundamental elements of revolution, namely, the process whereby the potential for revolution is translated into the ordered application of arms. This process will be described in this paper as *The Factors of Revolt*. (See Fig. 1).

Accepting the CPM's theoretical kinship with a select few from the pantheon of Communist revolutionary theorists, it is appropriate that its revolutionary Theory and Practice should be analysed against their prescriptions.

It follows therefore that the frame of reference for this analysis, *The Factors of Revolt*, owes much in its creation to the Marxist-Leninist, Stalinist and Maoist theories of revolution. It needs also to be said that this frame of reference was developed to accommodate the considerable variation in the Theory and Practice of the aforementioned.

The question of language and terminology that has changed its meaning and, significantly, its interpretation, has presented the international Communist movement with a legacy of theoretical confusion. The ongoing doctrinal debate amongst Marxists of all persuasions is notable for both its complexity and disputatious nature. These complexities have served to confuse and frustrate a generation of scholars of Communist theory. One such scholar was moved to proclaim:

> Their doctrine combines a religion and eschatology of salvation; a vast accumulation (from pre-1848 to the present) of political commentary and judgements, most of them out of date if they were ever valid; an economics now irrelevant; a historical sociology and critique of economic and social institutions, much of which is still suggestive; a philosophy which is little more than verbal casuistry. To make matters worse, every assertion in the voluminous, contradictory writings of Marx, Engels and Lenin is held up to be part of a single science, a canon of which any sentence may be treated as having probative value. (Wolfe 1962-3:158)

Quite obviously it is beyond the scope of this essay to present a detailed analysis of the semantics, theses and interpretations that constitute the conformable basis of Communist revolutionary theory. Such an analysis will be included in the writer's completed research. *The Factors of Revolt* herein presented is a synthesis of the salient features of these diverse theories thereby providing a basis for detailed analysis of individual Communist revolutions.

In deference to both Wolfe and Plamenatz, it is hoped that the limited frame of reference defined by this paper will not add too much to the general confusion of the genre.

DISCUSSION

Assumptions

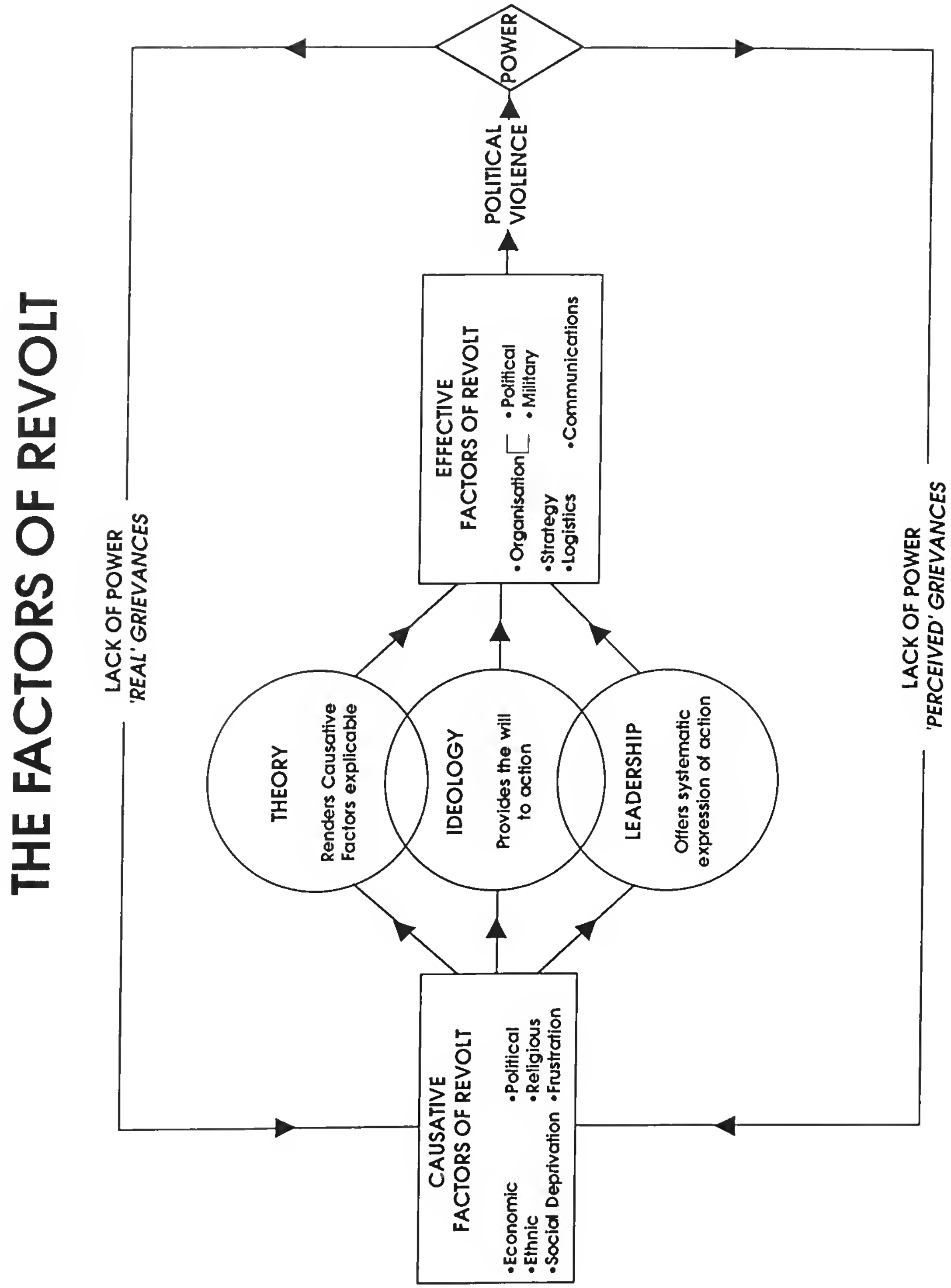
In discussing the pursuit of power, Hans Morgenthau argued that it is a characteristic of all politics that participants usually seek recourse to a set of moral arguments which serve to justify and legitimise the course of action being undertaken:

> '... the element of power as the immediate goal of the policy pursued is explained and justified in ethical, legal or biological terms. That is to say: the true nature of the policy is concealed by ideological justifications and rationalisations.' (Morgenthau 1973:89)

If these justificatory arguments are integral to the pursuit of power, it follows that they must also be integral to the understanding of the nature of revolution.

Revolutions do not simply occur.

A revolution represents an extreme form of political disagreement. It signifies the withdrawal of one of the parties from the constitutional forum with the object of achieving a radical *transformation* of the political system far beyond the limited goals available through the constitutional process.



This objective is pursued through the ordered application of political violence.

Such violence can only be fomented through the manipulation of the raw potential for revolt - those diverse and often diffuse elements that comprise the base for dissatisfaction, such as grievances based on psychological, economic, social, political, ethnic and religious grounds. Clearly distinguished from incidents of particularised violence,

such as communal, industrial, religious and so forth, revolutionary activity is the successful translation of all the potentially destabilising forces within society into a *total*, extralegal challenge to power. This challenge has, as its basis, clearly defined objectives regarding the pursuit and exercise of power and the nature and form of the new society.

The nature of revolution in general and the essence of Communist revolutions in particular, is given eloquent expression in Mao Tse tung's aphorism on the subject:

> 'A revolution is not a dinner party, or writing an essay, or painting a picture, or doing embroidery; it cannot be so refined, so leisurely and gentle, so temperate, kind, courteous, restrained and magnanimous. A revolution is an insurrection, an act of violence by which one class overthrows another.' (Mao Tsetung 1966:11)

Within the Marxist view of history, revolution represents a legitimate process of accelerated change and is, therefore, to be actively encouraged:

> 'Both for the production on a mass scale of this Communist consciousness, and for the success of the cause itself, the alteration of men on a mass scale is necessary, an alteration which can only take place in a practical movement, a **revolution**; (sic) this revolution is necessary, therefore, not only because the ruling class cannot be overthrown in any other way, but also because the class overthrowing it can only in a revolution succeed in ridding itself of all the muck of ages and become fitted to found society anew. (Mark-Engels Vol. 1. 1977:41)

Thereby revolutions become "... the locomotives of history." (Marx-Engels Vol. 1. 1977:277)

The question facing all potential revolutionaries, Communist or otherwise, is how to make a revolution occur, and, significantly, how to control and direct it once it has occurred.

Twentieth century revolutionary practice has as its inspiration the rich gallery of nineteenth century Russian anarchism. Robert Payne, in his *Life and Death of Lenin*, suggested that Lenin was quick to acknowledge his debt to one of the more sinister figures of the Russian revolutionary hagiography, Sergei Nechayev. (Payne 1964:34)

Anarchist, revolutionary and author of the *Revolutionary Catechism*, Nechayev advocated the application of ordered violence aimed at the total negation of the state through the activities of a conspiratorial elite of professional and committed revolutionaries:

> 1. The revolutionary is a doomed man. He has no personal interests, no attachments, no property and no name. Everything in him is wholly absorbed in the single thought and the single passion for revolution.

and

> 22. By a revolution the Society does not mean an orderly revolt according to the classic western model - a revolt which always stops short of attacking the rights of property and the traditional social systems of so called civilisation and morality. Until now such a revolution has always limited itself to the overthrow of one political form in order to replace it with another, thereby attempting to bring about a so-called revolutionary state. The only form of revolution beneficial to the people is one which destroys the entire state to the roots and exterminates all the state traditions, institutions and classes in Russia. (Payne 1964:24-28).

The Revolutionary Catechism represented a break with the anarchist tradition that linked revolution with individual acts of terrorism. It provided both a *modus operandi* for conspiratorial action and a code of ethics which effectively elevated the notion of revolution as an end in itself. To these ethics Lenin was to introduce the idea of political organisation. Given his single mindedness on the matter and the indisputable success of his stratagem, it is hardly surprising that Lenin found himself subject to accusations and abuse from his political opponents for employing "Nechayevist" methods. (Trotsky 1972:27).

Lenin also claimed to be a faithful exponent of Marx's revolutionary theory:

> 'The necessity of systematically imbuing the masses with **this** (sic) and precisely this view of violent revolution lies at the root of the **entire** (sic) theory of Marx and Engels.' (Lenin 1969:22)

Discussing the historical context of revolutionary development, Lenin defines his understanding of the basis of Marxist theory:

> 'True to his philosophy of dialectical materialism, Marx takes as his basis the historical experience of the great years of revolution, 1848 to 1851. Here, as everywhere else, his theory is **summing up of experience**, (sic) illuminated by a profound philosophical conception of the world and a rich knowledge of history.' (Lenin 1969:28)

Part of this 'conception of the world' was the Marxian unity of Theory and Practice. Transposed into Lenin's terms, theory, in 'summing up experience', was of no value unless it offered a programme of action. Theory had to be dynamic as form (*i.e.* reality,) was ever changing.

In *What is to Be Done?*, sub-titled 'Painful Questions of Our Movement;' Lenin critically examined the political opposition in Russia, the potential revolutionary forces in Russia and the actual revolutionary activity in the country. He found all three areas wanting.

Suggesting that there was little to support the theory that the proletariat had any potential for being a *spontaneous* revolutionary force, and caustic in his criticism of the apparent inertia of the 'economists' and the naivette of the 'primitivists', Lenin posed the following:

> 'Why do the Russian workers still manifest little revolutionary activity in response to the brutal treatment of the people by the police ... We must blame ourselves and our lagging behind the mass movement for our still being unable to organise sufficiently wide, impressive and rapid exposures of all the shameful outrages.' (Lenin 1988:135-136)

He concluded that effective organisation was the key to leading the proletariat along the path towards revolution.

In *What is to Be Done* and subsequent works, including his *Two Tactics of Social Democracy in the Democratic Revolution* (1905) and his *April Thesis* (1917), Lenin extended his analyses into a prescription for revolutionary organisation centred around the transformation of the inertia of the masses into revolutionary activity. Abandoning the ideal of spontaneous mass uprising, he, like Nechayev, argued in favour of a highly centralised underground political movement comprised of dedicated (and professional) activists and revolutionaries that would engineer revolution and seize power in the name of the workers. This was to be achieved through centralised political organisation; resolute and unquestioned leadership; thorough political training and, of course, total commitment and unity of purpose:

> 'I assert: (1) that no revolutionary movement can endure without a stable organisation of leaders maintaining continuity; (2) that the broader the popular mass drawn spontaneously into the struggle, which forms the basis of the movement and participates in it, the more urgent the need for such an organisation, and more solid this organisation must be (for it is much easier for all sorts of demagogues to side-track the more backward section of the masses); (3) that such an organisation must consist chiefly of people professionally engaged in revolutionary activity; (4) that in an autocratic state, the more we **confine** (sic.) the membership of such an organisation to people who are professionally engaged in revolutionary activity and who have been professionally trained in the art of combating the political police, the more difficult will it be to unearth the organisation; and (5) the **greater** (sic.) will be the number of people from the working class and from the other social classes who will be able to join the movement and perform active work in it.' (Lenin 1988:185)

Lenin was scathingly critical of any method other than that which he prescribed:

> 'A person who is flabby and shaky on questions of theory, who has a narrow outlook, who pleads the spontaneity of the masses as an excuse for his own sluggishness, who resembles a trade-union secretary more than a tribune of the people, who is unable to conceive of a broad and bold plan that would command the respect even of opponents, and who is inexperienced and clumsy in his own professional art - the art of combating the political police - such a man is not a revolutionary, but a wretched amateur!' (Lenin 1988:188)

It needs be said that not all Russian Marxists were enamoured with either Lenin or the Bolsheviks. Many remained chary, recognising that Bolshevism held within itself the

seeds of dictatorship. On November 7 1917, writing in *Novaya Zhizn*, Maxim Gorky gave expression to this fear:

> '... but I believe that the good sense of the working class and its awareness of its historical tasks will soon open the eyes of the Proletariat to the utter impossibility of realising Lenin's promises, to all the depth of his madness, and to his Nechaev and Bakunin brand of anarchism... Does the Russian democracy remember the ideas for the triumph of which it struggled against the despotism of the monarchy? Does it consider itself capable of continuing this struggle now? Does it remember that when the Romanov gendarmes threw its ideological leaders into prisons and hard-labour camps, it called this method of struggle base? In what way does Lenin's attitude towards freedom of speech differ from the same attitude of a Stolypin, a Pleve, and other half-humans? Does not Lenin's government, as the Romanov government did, seize and drag off to prison all those who think differently?' (Gorky 1968: 85-86)

Nonetheless, Bolshevism was to beget a new canon in the eschatology of revolution - the notion of scientific revolution which had, at its core, a vanguard party '... guided by the most advanced theory.' (Lenin. 1988:92) And, although subsequent Communist theoreticians modified Lenin's theories to suit their particular 'objective' conditions, his prescriptions on transforming the inertia of the masses through theory (organisation), ideology and leadership became the hallmark of international Communist revolutionary theory after the Bolshevik seizure of power in 1917.

The interplay between the theory and practice of revolution was given further expression by Stalin, who, elaborating upon Lenin, stated that:'Theory is the experience of the working-class movement in all countries taken in its general aspect. Of course, theory becomes purposeless if it is not connected with revolutionary practice, just as practice gropes in the dark if its path is not illuminated by revolutionary theory.' (Stalin 1970:22)

In his famous refutation of Kautsky's critique of Bolshevism, Trotsky answered his own rhetorical question about the importance of theory and ideology:

> 'Is there still theoretical necessity to justify revolutionary terrorism? Unfortunately, yes. Ideology, by its very essence, plays in the Socialist movement an enormous part. Even for practical England the period has arrived when the working class must exhibit an ever-increasing demand for a theoretical statement of its experiences and its problems.' (Trotsky 1969:9)

And, underscoring the role and significance of ideology in maintaining requisite revolutionary fervour and commitment, Kim Il Sung urged that:

> 'We should educate and reform all Party members and working people in Marxist-Leninist ideology so that all the labouring masses in the northern half fight on with a firm faith in Communism.' (Kim Il Sung 1971:91)

Finally, for Mao Tse-tung, authority and leadership, the keystone of Communist revolutionary theory and practice, remained with the Party:

> 'If there is to be a revolution, there must be a revolutionary Party. Without a revolutionary Party, without a Party built on the Marxist-Leninist revolutionary theory and in the Marxist-Leninist revolutionary style, it is impossible to lead the working class and the broad masses of the people in defeating imperialism and its running dogs. (Mao Tse-tung 1966:1)

It may be accepted therefore that theory, ideology and leadership are intrinsic to the practice of Communist revolution. Theory is the "expression" of experience; ideology provides the sustaining myth to follow and without theoretically and ideologically sound leadership "it is impossible to lead the working class and the broad masses of the people."

Factors of Revolt

The symbiotic relationship between theory, ideology and leadership adds credence to Morgenthau's "ideological justifications and rationalisations." For Communist revolutionaries, theory becomes an important justificatory measure, laying the foundations for revolt and a method for achieving it in the name of a higher social order. Ideology provides the world view and legitimacy for revolt and the unimpeachable vanguard party,

built upon and guided by that theory, provides the focus for revolution.

Developing this concept, the Communist perspective of revolution can be understood through an analysis of what this paper will describe as the relationship between the **Causative Factors** and **Effective Factors** of Revolt.

The Causative Factors are those complex elements that comprise the basis of dissatisfaction, namely grievances based on psychological, economic, social, political, ethnic, religious factors and so on. These are usually associated with a real or perceived alienation from, and oppression by, the power *i.e.* the State. Brought together, these elements have the potential to inspire revolt.

Should these elements be harnessed through the intermedia of **Theory**, **Ideology** and **Leadership**, they are translated into the Effective Factors of Revolt that comprise the practical manifestations of political violence, namely military and political organisation, strategy, logistics, communications, propaganda and so forth. These factors serve to implement the ordered application of such violence.

The theoretical foundations of political violence provide the medium through which the Causative Factors may be legitimised, serving as a course of action for revolutionary activity. In turn, these foundations are moulded into Effective Factors through the development of cogent ideologically based arguments and policies and sound leadership.

A revolutionary group needs to articulate, mobilise and sustain support for its cause. This can only be achieved by transforming the Causative Factors of Revolt into Effective Factors through the aforementioned symbiosis of theory, ideology and leadership.

Theory renders the Causative Factors explicable, ideology provides the will and impetus to action and leadership provides the systematic expression of action.

It is, therefore, incumbent upon the revolutionary group to provide appropriate expression to the "experience" of those it purportedly leads. This expression, in turn, should be articulated through cogent ideological argument to mobilise committed and organised support for revolution.

Finally, the transformation of this revolutionary support into revolutionary action (Effective Factors) is achieved through both the theoretical (vanguard) and personal (charismatic) components of leadership. (Coe 1986:67).

Should these components be synchronous, the Effective Factors are likely to coalesce as a co-ordinated challenge to power, reflecting the diffuse grievances from which it developed.

In analysing Communist revolutions, the Factors of Revolt provide a general frame of reference for testing the applicability of the revolutionary party's theory, ideology and leadership against both the foundations and practice of its revolt.

Proposition

During its challenge to power in Malaya, the Malayan Communist Party set great store in applied theory:

> 'There is no substitute for diligent and constructive study of Marxist-Leninist theory. Without a sound and daily reinforced ideological foundation, the ability to perceive, discern and act cannot but be unequal to the task at hand. Two trends - both equally harmful - in the field of theoretical studies should be combated. One is the trend of intellectual abstractionism - so common and baneful among those with a bourgeois academic background. This trend manifests itself in a kind of arrogant detachment from persons and events that are integral parts of the Revolutionary movement. A look around the Marxist-Leninist Parties that have failed, in contrast to those that have succeeded, will readily show how futile a Party led by intellectual abstractionists can become in relatively short time. The other trend is that of 'intellectual slumming'; that is, a brand of petty-bourgeois sentimentality which says, in effect, that the working class can do no wrong and, therefore, needs no theories. People who talk and work like that should not complain when they find themselves at the head of a neo-Fascist movement comprised of a horde of the dirtiest lot of *lumpen* degenerates from the working class and the peasantry who ever scorned theory." (CPM 1965:11)

The Party also claimed to be at the vanguard of the revolution:

> 'On the one hand, the Liberation Army is being led by the Communist Party, true to the doctrines and spirit of Marxism-Leninism, and is thus able to learn during the course of the struggle, to take advantage of the lessons of the revolutionary wars in other lands throughout the world -...' (CPM 1948)

The Malayan Communist Party failed in its revolt. Its failure can be attributed to several factors, not least being the intractability of the government in the face of challenge - an intractability evidenced by political will; sound political, civil and military intelligence supported by superior military strength and, ultimately, the ability to carry popular support.

But also and by its own definition, the Party's failure might be adduced to either a lack of diligent study, too many futile abstractions, too much 'intellectual slumming' or its failure to take advantage of lessons of other revolutionary wars. These issues beg the question as to whether the revolutionary practice of the Party was an accurate reflection of its theory.

These abstractions will be tested against the Factors of Revolt.

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VISITOR EXPERIENCES AND PERCEPTIONS OF THE FANNIE BAY GAOL MUSEUM

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ABSTRACT

Three hundred and ninety-four visitors to the Fannie Bay Gaol Museum were surveyed to ascertain their response to and evaluations of this Museum. Visitors rated the Fannie Bay Gaol Museum on perceived informativeness, enjoyment, excitement, and authenticity, as well as making judgements about subjective learning, actual exit knowledge, and reactions to various facets of the Museum. The Museum was rated highly on the four evaluative dimensions, with perceived authenticity being found most prominent. The ratings of various visitor subgroups are also explored, along with the implications of the association between subjective learning and high ratings on the evaluation dimensions for future museum research.

KEYWORDS: Museum evaluation, enjoyment, excitement, authenticity, informativeness, exit knowledge, Fannie Bay Gaol Museum, visitor evaluation, subjective learning.

INTRODUCTION

The Fannie Bay Gaol Museum, Darwin

The Fannie Bay Gaol Museum in Darwin contains the greater portion of what served as one of the few penal institutions in the Northern Territory over the period since first European settlement. Funds for the erection of a new "Gaol and Labour Prison" were authorised by the South Australian Government in 1881 and tenders were called a year later for the building of the first cell blocks. Various additions and alterations were made over the years until the Gaol finally closed in 1979. Over the years of its operation the Gaol developed associations with virtually every aspect of the Northern Territory's cultural and political history. At the time of its closure its relative intactness and the survival of details of its use in both its fabric and fittings enabled it to retain a powerful penal atmosphere and to demonstrate prisoners' routines and living conditions. Within its perimeter could be found structures dating back to 1883 and others of more recent origin, all of which demonstrated adaptions of penal design to accommodate Territory conditions and resources. The roll call of Fannie Bay prisoners, actual or fictional, made it one of the best known gaols in Australia. Perhaps of most importance, the existing structures, remains and adjacent areas provide not just an important historical resource for scholars but a place of considerable interest to the public (Forrest 1979; Kerr 1981).

Shortly before the Gaol's last prisoners left in September, 1979, the Northern Territory Government publicly announced that it wished to put the gaol site to some new and worthwhile use. The Ministers of Community Development and Lands and Housing sought suggestions, and in response a number of submissions and comments were made. In November that year the National Trust of Australia (Northern Territory) was formally engaged as a Government consultant to make recommendations for the future of the site. Two Trust reports were presented to the Department of Community Development, the first in December 1979, and the second in November 1981. In the meantime, in May 1980 the Trust was appointed "to develop and manage the site as a place of historic interest". The appointment was "to be subject to a further

cabinet consideration of a satisfactory proposal... to manage the project". The Trust's final recommendations in 1981 were detailed but they essentially proposed that the general conservation policy should be to retain the Gaol's structures and spaces as they were, and by the recovery of missing contents, to work the Gaol precinct gradually up to the state it was in during its last period before closure. It was also recommended that the general presentation and interpretation policy should be to enable the public to understand most of the uses of the spaces and features without intrusive explanatory material (Forrest 1979; Kerr 1981).

After more than a year's consideration, in December 1982, the Government rejected the Trust's proposals and decided instead that the Gaol site should be managed by the Museums and Art Galleries Board of the Northern Territory in a very different way. The Board took over control in early 1983. Its plan for the Gaol, which has since been implemented, involved division of the Gaol site into two distinct sectors to preserve the intrinsic character of some of the site, whilst incorporating general displays of Territory history and technology. One, comprising cell blocks, ablution areas, exercise yards, kitchen and dining areas and other buildings, was presented to visitors as it had been when in use as a gaol in 1979, but with the addition of signs and various exhibits and the removal of demountables. A second zone, part of the former stores area, was turned into a transport display, which includes a locomotive and carriage, and a home of various displays relating to Cyclone Tracy, which almost destroyed Darwin in December 1974. There was some argument among historians and conservationists about the Gaol's presentation. The Museums and Art Galleries Board, however, argued that the National Trust's plan was too narrow and that under Board control the Gaol site would provide a much more enjoyable and educationally worthwhile experience for visitors. The Gaol is now one of the most popular attractions in Darwin for tourists and is also visited by many Darwin residents. The present research seeks to discover how visitors evaluate this site.

Museum Research

Research on the educational effectiveness and enjoyment of museums and exhibitions has been a prominent feature of work within the fields of communication and design for a number of decades now. Within the discipline of Psychology, notions such as right-handed bias, exit phenomenon-exit gradient, and information overload/museum fatigue have long been the subject of investigation and comment. The right-handed bias effect refers to the tendency of visitors to museums to turn right upon entering a gallery or exhibit hall and move around in that direction (Robinson 1928; Melton 1972). The exit phenomenon or exit gradient refers to the tendency of visitors to use the first exit they encounter in a museum and in so doing often miss parts of the museum (Parson and Loomis 1973). Museums have been found to produce information overload and hence museum fatigue, if for example, the exhibits are too complex or it is difficult to move around easily among the various displays (Melton 1972). Melton also found that once inside a museum people stop at the first few exhibits and then become more selective, stopping at fewer the longer they explore. Melton also made the point that those items or displays which are then observed tend to hold greater interest for the visitor. The degree of interest here Melton termed attraction gradient.

Measurement of Visitor Reactions

Perhaps the most popular form of instrument in the assessment of tourist feedback is the visitor questionnaire, usually a pencil-and-paper measure completed by guests around the time of departure. Lewis and Pizam (1981) have written that this technique provides a quick measure of overall guest satisfaction, that it can identify dimensions in which satisfaction or dissatisfaction occurs, and that it can identify individual determinants that comprise each dimension and which might be the specific causes of satisfaction or dissatisfaction. They argue that the questionnaire is easily completed by most guests, and may be speedily tabulated and analysed by management. Lewis and Pizam further argue that the result may be a valid and reliable method for rating management, locating operational malfunctions, ascertaining guests' needs and comparisons among leisure installations, and gauging improvements or deteriorations over time. Finally Lewis and Pizam hold that the survey instrument should be used with some caution, operationalising more sophisticated concepts in questions, and generally

employing the more powerful analysis techniques such as multivariate analyses. Pearce and Moscardo (1984) make the point that the study of tourist complaints and negative experiences is also an appropriate method within the context of tourist evaluation. They have written that tourists' complaints are most often collected by way of techniques such as visitors' books, guest cards and questionnaires, along with interpersonal contact with staff.

Evaluation of Specific Sites

Pearce and Moscardo (1985), in a thorough and wide-ranging paper focussing on visitor evaluation, investigate a number of evaluation contexts. At the beginning of the paper, Pearce and Moscardo make the point that within visitor evaluation two components may be distinguished: visitor profiles and visitor reactions. Visitor profiles have traditionally been the favoured aim for many proprietors or guardians of a recreational area who want to know more about the people who use their facility. However visitor reactions are increasingly seen as important, for they reflect tourists' cognitions, their satisfactions and emotional reactions to the specific tourist venue, and it is this type of evaluation upon which this paper will focus.

Pearce and Moscardo have examined the research evidence associated with visitor centres in various contexts and locations. They report that visitor centres are usually constructed adjacent to the venue of interest, and often are a prelude to visiting the park or environment itself. They hold that exhibits in a visitor centre are meant to interpret, to comment upon and stimulate interest and enjoyment in the environment the tourist is about to visit. They argue that the chief aim of the visitor centre is interpretation, which may be defined as the stimulation of tourist interest and enthusiasm, and the educational or pedagogic supplement to satisfy that interest.

They cite the work of Washbourne and Wagar (1972) who studied four United States visitor centres, and emphasised in their conclusions the importance of factors such as visitor interest, dynamic presentations, violent subject material and holistic presentations. Washbourne and Wagar found that these four factors make for successful interpretation to visitors. Pearce and Moscardo also cite the research of the Countryside Commission (1978) in the United Kingdom. This work utilized a psychological framework in its assessment of visitor centres, and recognized that the central product offered by any tourist location is "experience", a point emphasised by commentators such as Iso-Aloha (1980).

The Countryside Commission looked at visitor understanding, enjoyment, and motivation, and attempted to relate these factors by way of the examination of display variables and visitor demographics. One of the findings of this study was that enjoyment and understanding are apparently relatively unrelated: people may enjoy their visit to a tourist site without necessarily learning a great deal from it. The study also found that the greatest amount of learning occurred at historical centres, whereas high levels of enjoyment were reported by the visitors at all centres. The highest enjoyment was reported at those locations where visitors could inspect the site as well as learn about it in the interpretation centre.

The study further found that factors such as size and layout of the centre, the provision of an audio-visual programme or the theme of the centre did not seem to relate to visitor enjoyment. The centres that motivated visitors to learn more about the park or venue were usually large and used a number of different types of interpretation. Finally Pearce and Moscardo report that animated, physically involving dynamic displays were found to be most effective in capturing the attention of all ages and social backgrounds.

Authenticity

Tysoe (1985) has written of the widespread belief that tourists are basically shallow and foolish individuals, typically satisfied with superficial, staged, inauthentic glimpses into the life of the country or region they are visiting. She has argued that this is a stereotype which is revealed to be generally untrue upon closer inspection. She cites the work of the American sociologist, MacCannell, who argued that many tourists are aware that their travel experiences are sometimes inauthentic, and often seek out more authentic experiences such as genuinely participating in the daily lives of the local inhabitants. Pearce (1982) and Pearce and Moscardo (1986) have cited a number of examples in support of this authenticity quest on the part of many tourists. They

have found that a few detailed and satisfying contacts with local people enabled many visitors to believe that they were going beyond the staged and superficial to a more genuine and authentic plane. Perceptions of authenticity, therefore, may well be an important criterion within the domain of tourist evaluation.

Research Questions

Questions associated with the issues of enjoyment and learning, with notions of authenticity, with informativeness and with levels of subjective learning as they all touch upon visitor behaviour at a site such as the Fannie Bay Gaol Museum are only just beginning to be explored (Pearce and Moscardo 1985). This research is directed at elucidating some of the relationships among these various notions by means of questionnaire-based interviews of individuals who have just visited the Fannie Bay Gaol Museum. Specifically, the aims of this research are:

1. To assess visitors experiences and interest in this site;
2. To assess the degree to which the visit was perceived as subjectively informative, exciting, enjoyable, and authentic as an historical tourist site;
3. To identify a range of variables which might be systematically associated with the evaluative dimensions of authenticity, enjoyment, excitement and informativeness.

METHOD

A total of 399 subjects were interviewed in the course of the study. Approximately 52% were male and 48% female, their ages ranging from 16 to 83 years. The median age was 39 years. Tourists, including foreign visitors, constituted a large proportion of the sample, comprising 77% from interstate, 10% from overseas, and 13% from the Northern Territory.

A questionnaire based on that used by the Countryside Commission (1979) was devised by the authors for the purpose of the study (Appendix I). The instrument aimed to elicit visitor responses to, and perceptions of, the Fannie Bay Gaol Museum. Various questions served to generate a visitor profile, and to assess visitors' past experiences with, interest in, and motivation to visit the site. As well as the evaluative dimensions of enjoyment, excitement and authenticity, two informational measures were included: one asked the respondents to rate the Fannie Bay Gaol Museum on its informativeness as an historical museum, whilst the other asked respondents if they believed they had learned something as a result of their visit to the museum. Further variables of interest in this particular study were demographic characteristics such as place of origin, age, and educational level of respondents, together with time spent at the museum and history of previous visitation.

A knowledge index, termed exit information, was also employed in this study. This index was based on twelve knowledge questions about the site and its history. Whilst it is not primarily a measure of information gained whilst on that visit to the Fannie Bay Gaol Museum, it is a measure of information recalled about the centre on exit, and may be related to notions such as enjoyment, just as information gain has been found to be.

Interviews were conducted on weekdays and weekends during May and June of 1987, during the Museum opening hours of 10.00am to 5.00pm. The interviewers (final year psychology students at the Darwin Institute of Technology, and ranging in number from 2 to 4 on different occasions), located themselves at the entrance to the Fannie Bay Gaol Museum, equipped with clipboards, pens and questionnaires. Subjects were selected on the basis of being the next person to make an exit, as an interviewer became available to request their co-operation in the study. An exception to this selection process was the visitor travelling via tour bus, who though willing, was generally too hard-pressed for time to be interviewed. Because of language interpretation problems, occasionally non-English speaking tourists were also excluded.

RESULTS

This section will present results from an examination of the various attitudinal, demographic and knowledge questions included in the survey. Results will be presented by way of frequency counts of the various response types for each question, bivariate analyses involving the various origins of the visitors, and multivariate analyses aimed at identifying predictor variables associated with the evalu-

ative domains of enjoyment, authenticity and informativeness.

Frequency Analyses

A. Length of visit. Respondents were asked how long they had stayed at the site. Table 1 shows that approximately half of the respondents recorded having stayed over 30 minutes, and three-quarters stayed at least 20 minutes. Most respondents stayed for about one hour or somewhat less, 46 minutes to one hour was the preferred length of visit.

Table 1: Duration of Visit to the Fannie Bay Gaol Museum.

Duration of Visit	Frequency	Percentage	Cumulative Percentage
5 mins or less	3	.8	.8
6-10 mins	1	.3	1.1
11-15 mins	8	2.0	3.1
16-20 mins	18	4.5	7.6
21-30 mins	80	20.2	27.8
31-45 mins	75	18.9	46.7
46-60 mins	98	24.7	71.4
61-90 mins	79	19.9	91.3
> 90 mins	34	8.7	100.0

N-399

B. Reactions to Facets of the Museum. This section concerns respondents' reactions to various aspects of the site. The first question asked respondents if they looked at the numerous displays of memorabilia during their visit to the museum.

Table 2: Number of Visitors who looked at All or Parts of Displays.

Displays Viewed	Frequency	Percentage	Cumulative Percentage
All	342	85.7	85.7
Parts	30	7.5	93.2
Unsure/Don't Know	27	6.8	100.0

N=399

Table 2 shows that the great majority (85.7%) of respondents believed they had looked at all of the displays, whereas only 7.5% looked at parts but not all. It is also surprising that 6.8% were unsure or did not know whether they had looked at all or parts of the displays.

A question was also included about the Cyclone Tracy Display.

Table 3: Numbers of Visitors who did or did not see the Cyclone Tracy Display

Attention to Display	Frequency	Percentage	Cumulative Percentage
Viewed Display	302	77.2	77.2
Did not View Display	89	22.8	100.0

N=391; Missing=8

From the above it can be seen that over 75% of respondents did see the Cyclone Tracy Display, with 22% missing or omitting it during their visit.

Respondents were asked whether they agreed with the present arrangement of the museum, wherein three different themes were presented: that of the historical gaol, a transport section, and the Cyclone Tracey Display. Table 4 contains the results for this question.

Table 4: Opinion of Appropriateness of Three Separate Themes at Museum.

Opinion of Three Themes	Frequency	Percentage	Cumulative Percentage
Appropriate	363	91.0	91.0
Not appropriate	36	9.0	100.0

N=399

It is obvious that a great majority agree with the present arrangement, with only 9% disagreeing.

A similar question was also asked of the respondents, this time focussing on whether the visitors would prefer the Fannie Bay Gaol Museum to concentrate solely on the history of the gaol.

Table 5: Visitors' Preferences for History of Gaol as Only Theme.

Preference	Frequency	Percentage	Cumulative Percentage
History only	34	8.5	8.5
Other Themes Okay	364	91.5	100.0

N=398; Missing=1

Results obtained here were similar to those from the previous question, with only 8.5% of respondents registering preference for only the history of the Fannie Bay Gaol.

C. Staff Visitor Contact. Respondents were asked about their contact with and perceptions of staff of the museum. Table 6 records the number of respondents who spoke to a staff member during their visit.

Table 6: Visitor Interaction with Staff Members.

Level of Interaction	Frequency	Percentage	Cumulative Percentage
Spoke with Staff	22	5.6	5.6
Did not Speak with Staff	372	94.4	100.0

N=394; Missing=5

It can be seen here that the vast majority of visitors did not speak with a staff member, with only 5.6% indicating that they did do so.

Respondents were asked how helpful the staff were.

Of the people who did have contact with a staff member, most found it a helpful contact. Only one respondent indicated not being helped by a staff member.

Table 7: Visitor Ratings of Helpfulness of Staff.

Rating of Helpfulness	Frequency	Percentage	Cumulative Percentage
Very Helpful	16	4.0	4.0
Fairly Helpful	2	.5	4.5
Not Very Helpful	1	.3	4.8
No Answer/Not Applicable	380	95.2	100.0

N=399

Respondents were also asked about the availability of a museum staff member to answer questions whilst they were at the museum. Table 8 presents their answers to this question.

Table 8: Visitor Beliefs about the Availability of Staff.

Rating of Availability	Frequency	Percentage	Cumulative Percentage
Staff Were Available	10	2.5	2.5
Staff Were Not Available	74	18.5	21.0
Don't Know	13	3.3	24.3
No Answer	302	75.7	100.0

N=399

A very small proportion (2.5%) believed that a staff member was available, a larger proportion (18.5%) believed that a staff member was not available. However the largest group of respondents (79.0%) did not know, were not sure, or could give no answer to the question.

Table 9: Knowledge about the Fannie Bay Gaol Museum and its Historical Context, as Assessed by the Knowledge Questionnaire.

Number of Correct Answers	Frequency	Percentage	Cumuative Percentage
1	0	0	0
2	3	.8	.8
3	5	1.3	2.1
4	15	3.8	5.9
5	28	7.1	13.0
6	43	10.9	23.9
7	29	7.3	31.2
8	67	16.9	48.1
9	70	17.7	65.7
10	73	18.4	84.1
11	44	11.1	95.2
12	19	4.8	100.0

N=396; Missing=3

D. Knowledge Questions. Included in the survey were a number of questions which attempted to assess the degree of knowledge a visitor has on leaving the museum. Whilst this is not necessarily a test of information gained during that particular visit, it does nonetheless give a measure of exit information concerning the Fannie Bay Gaol Museum.

Table 9 contains information on the twelve knowledge questions. From this it can be seen that whilst there were a number of respondents who managed to successfully answer only a few questions, 50% of the sample scored nine or more questions correct.

E. Overall Evaluation. Each respondent was asked to rate the Fannie Bay Gaol Museum according to a number of dimensions: Informative-Uninformative; Exciting-Dull; Enjoyable-Not Enjoyable, and Authentic-Artificial. Tables 10-13 contain the results of these evaluations.

Table 10: Informative-Uninformative Ratings of the Fannie Bay Gaol Museum.

Rating	Frequency	Percentage	Cumulative Percentage
1. Uninformative	2	.5	.5
2.	10	2.5	3.0
3.	108	27.1	30.1
4.	176	44.1	74.2
5. Informative	103	25.8	100.0

N=399

Table 11: Exciting-Dull Ratings of the Fannie Bay Gaol Museum.

Rating	Frequency	Percentage	Cumulative Percentage
1. Dull	16	4.0	4.0
2.	39	9.8	13.8
3.	196	49.4	63.2
4.	111	28.0	91.2
5. Exciting	35	8.8	100.0

N=397; Missing=2

Table 12: Enjoyable-Not Enjoyable Ratings of the Fannie Bay Gaol Museum.

Rating	Frequency	Percentage	Cumulative Percentage
1. Not Enjoyable	10	2.5	2.5
2.	17	4.3	6.8
3.	129	32.5	39.3
4.	142	35.8	75.1
5. Enjoyable	99	24.9	100.0

N=397; Missing=2

Table 13: Authentic-Artificial Ratings of the Fannie Bay Gaol Museum.

Rating	Frequency	Percentage	Cumulative Percentage
1. Artificial	1	.3	.3
2.	2	.5	.8
3.	31	7.8	8.6
4.	129	32.3	40.9
5. Authentic	236	59.1	100.0

N=399

The majority of individuals found the Fannie Bay Gaol Museum to be informative, somewhat exciting, enjoyable and authentic. It was the final dimension, that of authentic-

artificial, which evoked the most prominent results. Visitors rated this site as very high in terms of authenticity, and conversely low on artificiality.

Finally respondents were asked whether they believed that they had learned something as a result of their visit to the Fannie Bay Gaol Museum.

Table 14: Visitor Ratings of Perceived Learning Whilst at the Fannie Bay Gaol Museum.

Rating of Learning	Frequency	Percentage	Cumulative Percentage
Learning Occurred	354	88.7	88.7
No Learning Occurred	45	11.3	100.0

N=399

Most respondents (88.7%) indicated that they did learn something, though 11% expressed the belief that they had not learned anything as result of their visit.

Bivariate Analyses

This part of the Results section will consist of bivariate analyses focusing on the origin of respondents and the evaluative dimensions Enjoyable-Not Enjoyable, Informative-Uninformative, and Artificial-Authentic. Figure 1 contains a graphic representation from the first such analysis.

A number of trends appear to emerge here. First, relatively few people, either locals or visitors, rated a visit to the Fannie Bay Gaol Museum as not enjoyable. However locals were more likely to record a neutral rating than were interstate or overseas visitors, who were more likely to record higher levels of enjoyment than locals. Moreover, of the two visitor groups, interstate tourists were more likely to record an enjoyable experience at the Museum.

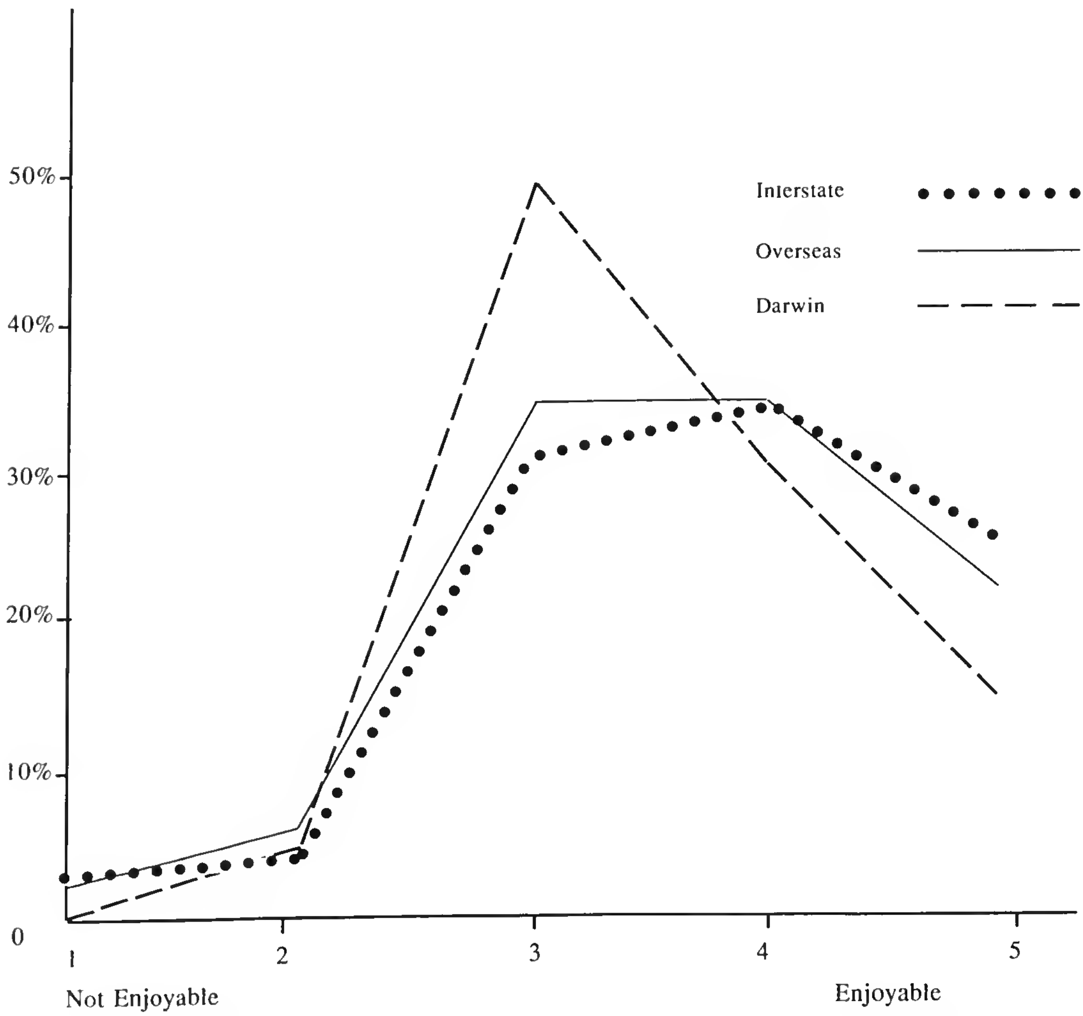

Figure 1. Local, interstate and overseas visitors' Enjoyable/Not Enjoyable ratings of the Fannie Bay Gaol Museum.

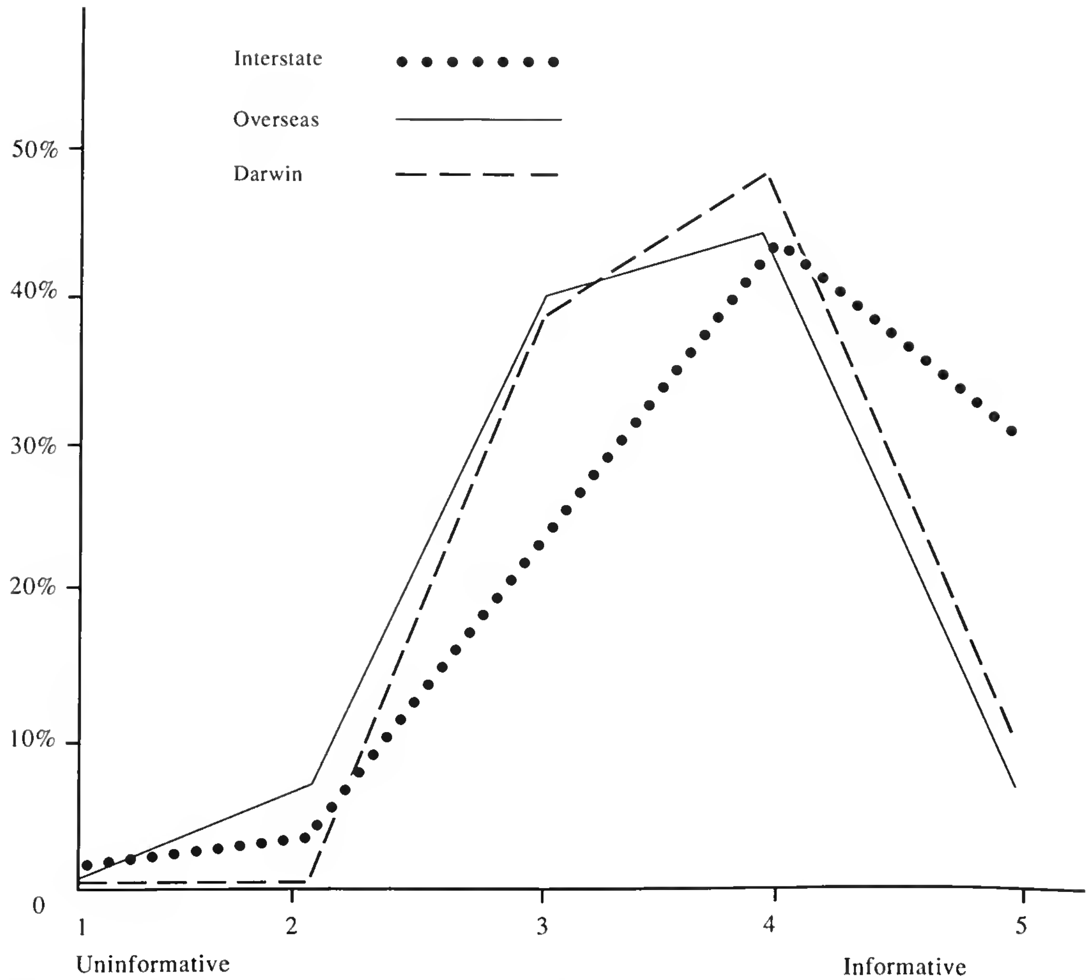

Figure 2. Local, interstate and overseas visitors' Informative/Uninformative ratings of the Fannie Bay Gaol Museum.

Figure 2 contains details of ratings relating to the informative nature of the visit. Few visitors would seem to leave this site believing that their experience was other than an informative one. However a high proportion of both local residents and overseas visitors recorded a neutral response, considerably more than the interstate visitors. Furthermore, at the highest informative rating, interstate visitors exceeded both local and overseas visitors by a ratio of at least 2:1. It is also worth noting that the lowest number of ratings at this level came from overseas visitors. It may be that many more overseas visitors recorded a neutral response either because of language problems or because they had been accustomed to more interactive museum environments in Europe and North America. Further research on this question would now seem appropriate.

The third figure (Fig. 3) represents visitors' ratings of the Fannie Bay Gaol Museum in regard to its perceived Authenticity-Artificiality. It is evident from this figure that a considerable majority of visitors see this as being a highly authentic site. The neutral category attracted relatively few ratings, though twice as many locals recorded a neutral rating as did interstate visitors. Most rated the Fannie Bay Gaol Museum as being somewhat authentic, with interstate and overseas visitors rating the Museum as being more authentic than did the locals. Here many more interstate and overseas visitors were likely to rank the Fannie Bay Gaol Museum at the highest level of authenticity than were local residents. It may well be that proximity leads to a lesser estimation of authenticity.

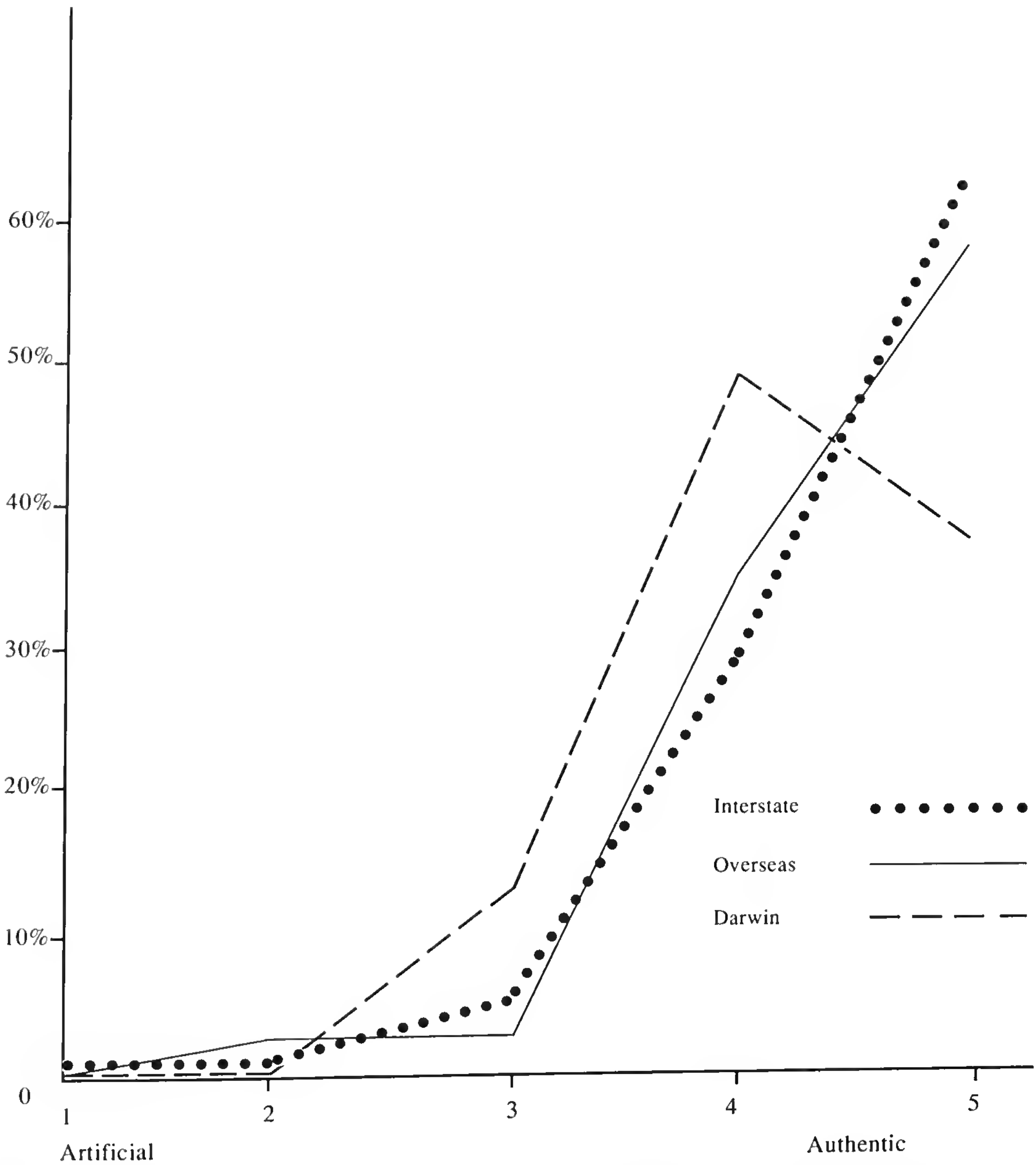

Figure 3. Local, interstate and overseas visitors' Authentic/Artificial ratings of the Fannie Bay Gaol Museum.

Multivariate Analysis

Four discriminant analyses were also employed in this study so as to highlight the variables that may predict those visitors more likely to rate the Fannie Bay Gaol Museum as being informative, exciting, enjoyable and authentic. The predictor variables included in each analysis included Intention to Visit, Type of Information Sought, Subjective Perceptions of Learning, Previous Visits to other Museums, Type of Visit, Age, Sex and Work Status.

From Table 15 it can be seen that two of the analyses, those involving ratings of informativeness and ratings of excitement, were significant at the .05 level, whereas the analysis of ratings of enjoyment was significant at the .1 level. The analysis involving ratings of authenticity did not produce a significant discriminant function. Table 16 contains the standardised canonical discriminant function co-efficients for each of the significant analyses.

From Table 16 it is apparent that the variable Subjective Learning is consistently asso-

ciated with informativeness, excitement and enjoyment. Those visitors to the Museum who believe that they have learned from their visit were likely to rate it highly as an informative environment and their visit as exciting and enjoyable. Males were more likely to regard this context as informative, whereas those visitors who had planned their visit and those who had come seeking specific information were more likely to regard their visit as exciting. Finally those in full-time work were more likely to report their visit as being enjoyable.

Table 15: Details of the Canonical Discriminant Functions for each of the four Analyses.

Criterion Variable from each Analysis	Canonical Correlation	Wilks Lambda	Significance Level
Informative	.2405	.9421	.0021
Exciting	.2634	.9305	.0162
Enjoyable	.1771	.9686	.0817
Authentic	.1043	.9891	.4628

Table 16: Standardized Canonical Discriminant Function Coefficients for Each Significant Analysis.

Predictor Variable	Informative Analysis	Excitement Analysis	Enjoyable Analysis
Subjective Learning	.72042	.71927	.72331
Sex	-.61066		
Intention to Visit		.57215	
Type of Visit		-.44926	
Work Status			-.7791

DISCUSSION

This report has examined a number of variables as they relate to tourist visitation to the Fannie Bay Gaol Museum. Various background characteristics of the visitors have been examined so as to produce a profile of the type of tourist who visits this site. Also examined were aspects such as length of visit, levels of exit information, staff visitor contact, and reactions to various facets of the Museum. Results were also presented on visitors' overall evaluations of the Fannie Bay Gaol Museum, and how Origin of Visitor varied along with type and degree of evaluation.

Overall, the Fannie Bay Gaol Museum has been evaluated positively by the majority of visitors in terms of criteria such as enjoyment, informativeness and authenticity. Whilst there was a tendency on the part of some overseas tourists to rate the site as being somewhat less than informative, and for the majority of visitors to be in some doubt as to whether a staff member was or was not available, these did not appear to be major factors hindering the overall appreciation of the visit. Rather they may be issues of fine-tuning and may involve exploration of ventures such as museum staff being available on occasions to answer questions, and the trial of interactive exhibits which include translations in the languages of the major overseas visitor groups.

The variable Subjective Learning has been revealed in this study as being consistently related to the domains of enjoyment, excitement and informativeness. Those individuals who perceive that they have undergone a worthwhile and profitable educative experience are the ones most likely to evaluate the context highly. It would thus seem of value to attempt to comprehend the types of museum experiences, contexts and components which do or do not make for judgements of subjective learning among visitors.

In conclusion, this study has produced a profile of visitor usage of the Fannie Bay Gaol Museum, and has revealed that the large majority of visitors, most often from interstate, view their visit in positive terms. As such, this historic venue would seem to be making a favourable impact on the overall experiences of those visitors to the Top End who include an outing to the Fannie Bay Gaol Museum as part of their holiday.

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APPENDIX

Condensed version of a questionnaire based on the Countryside Commission (1979), and modified by the authors for this study, to survey visitor experiences at the Fannie Bay Gaol Museum Darwin.

Interviewer Name
Date of Interview (day, month)
Time of start of interview
Weather at time of interview (sunny, overcast, rain)

1. Have you ever visited this museum before? If yes: (a) How many times have you been to the musum before? (b) How many times have you been here in the last 12 months?
2. Have you come to this centre alone or with some other people? If with others: (a) Have you come in an organised party or with friends and/or members of your family? (b) If in 'organised party' What sort of party have you come with? (c) Numbers in Group. (d) Have you come mainly because of your own interest in this museum, or because the people you are with wanted to come? (e) Have any of the people you are with been here before?
3. Did you intend to visit the Gaol Museum today, or were you just passing?
4. How did you first learn about the Fannie Bay Gaol Museum?
5. Did you have a general look round or did you look for something in particular? If 'particular': (a) What was it that you wanted to see? (b) Did you look round the displays? (c) Did you look at all of the displays or just parts of it? If 'parts': (d) Which parts did you look at? (e) Did you watch the video in the Cyclone Tracy display? If 'No': (i) Have you ever seen it? (ii) Did you know there was one here?
6. Did you come to the museum to ask for specific information or just to have a look round? If 'Specific information': (i) What was the information you wanted?
7. Did you talk to a member of the staff in the museum? If 'yes': (a) What was this about? If point of information (e.g. technical question): (b) Were the staff able to answer you question? (c) Were they: Very helpful, Fairly helpful, Not very helpful. (d) Was there a member of the staff available to answer questions whilst you went round the museum?
8. How long would you say you had spent at the museum?
9. When was this place first used as a prison? A. about 1860, B. about 1880, C. about 1900, D. about 1930, E. about 1950.
10. How much of the laundry building is still standing? A. The entire building, B. Most of the walls, C. Only the foundations.
11. Did this complex ever contain a section for juvenile offenders?
12. The maximum security section contains how many cells? A. 8 cells, B. 16 cells, C. 48 cells.
13. How many solitary confinement cells were there? A. 1, B. 2, C. 3.
14. Which section of the Gaol Museum has been converted into a series of historical displays? A. The mess, B. The laundry, C. The assembly area, D. The main guardroom.
15. Which section of the gaol was used for the last execution to take place in the Northern Territory? A. The maximum security section, B. The exercise yard, C. The infirmary.
16. In what year did the last hangings take place? A. 1939, B. 1952, C. 1968, D. 1979.
17. Who was the Police Inspector named in the historical display section? A. Leichhardt, B. Ayer, C. Foelsche, D. Palmerston.
18. Who was the well-known Aboriginal prisoner also named in this display? A. Kakadu, B. Tiwi, C. Nemarluk, D. Uluru
19. In the Cyclone Tracy display there appears a photograph of the man appointed to oversee the evacuation and clean-up of the city after the cyclone. Who was he? A. Paul Everingham, B. Alan Stretton, C. 'Tiger" Brennan.
20. In what year did this site cease being used as a gaol? A. 1970, B. 1975, C. 1979, D. 1982.
21. Do you know which organisation runs this gaol museum? If 'yes': (a) Could you give me the name? (b) What message do you think the organisation wants to get over to visitors?
22. Was there anything of interest to you at the gaol museum that you would now like to find out more about? If 'yes': (a) What is this? (b) Do you

think there is anything else that the gaol museum should provide information on? If 'yes': (c) What is this?

23. Do you agree with the idea of having three separate themes on display in the museum? (i.e. historical gaol, transport display, and cyclone display). Would you prefer the Fannie Bay Gaol Museum to solely concentrate on the history of the Gaol?
24. Do you feel that the way this gaol museum as set out and run could be improved or not? (a) In what way might it be improved? Please rate which comes closest to describing your visit round the gaol museum today, in the following categories. Informative - Uninformative, Exciting - Dull, Enjoyable - Not Enjoyable.
    Please rate which comes closest to describing the Fannie Bay Gaol Museum in the following category. Authentic - Artificial
25. Do you feel that you personally have learnt something new as a result of your visit to the gaol museum? If 'yes': (a) What have you learnt?
26. Have you visited any other museums like this one? If 'yes': (a) About how many museums have you visited?
27. How interested would you say you were in historical displays? Very interested, Fairly interested, Not very interested, Not interested at all. How interested would you say you were in this type of historical display? Very interested, Fairly interested, Not very interested, Not interested at all.
    (a) Would you say your interest was general or just in a particular aspect of the gaol museum? General, Particular.
    If 'particular': (i) What particular aspect of the gaol museum interests you?
28. Describe in a few sentences the most pleasant aspect or experience of your visit to the Fannie Bay Gaol Museum. Describe any unpleasant aspect or experience associated with your visit to the Fannie Bay Gaol Museum.
29. In order to check whether the information we have collected is representative, please give: (i) Home address, (ii) Set out today from... (if not Australia write country of residence).
30. Are you on a day trip from home, away from home on holiday, away from home for any other reason.
31. Age last birthday, Sex, Years of formal education.
32. Working Status: in full time, part-time employment, Housewife, Student, Retired, unemployed. What is/was your occupation? (If housewife record husband's occupation).

GENERAL COMMUNICATION

ABORIGINAL AND MAKASSAN RELATIONSHIPS

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ABSTRACT

This research note is a resumé of work completed on the history of the Makassan voyages to Australia since the seventeenth century and the relationships established between the Makassan sailors and the Aboriginal Communities. In addition it outlines current research into the nomenclature of Makassan camp sites and other places and presents the results of the work recently carried out in Groote Eylandt.

KEYWORDS: Aborigines, Arnhem Land, history, historic sites, Makassar-Makassans, Marege, perahus, place names, trepang.

INTRODUCTION

In this paper I wish to recount some of the research carried out over the last six years on what I call the Makassar-Marege connection. This research has covered the history of the Bugis Makassar people of South Sulawesi and the voyages carried out by fishermen to Marege or north Australia.

Studies have also been carried out into the type of vessel used on the voyages and the routes taken and the relationships between the Aborigines of Arnhem Land and the Makassan sailors. The study of genealogies of both Makassan and Aboriginal families has helped establish and renew the family ties broken in 1907.

In addition, I wish to identify and record the Makassan sailors' trepang processing sites, and other places.

BACKGROUND

Since the beginning of the seventeenth century, and probably long before, the fishermen of South Sulawesi from the Sultanate of Makassar have been recorded as sailing to Marege and Kayu Java to fish for the 'fruits of the sea', of which trepang has been one of the major items of commercial value (see Spillett 1987). The voyages reached as far as Cape York area of north Queensland and to King's Sound and beyond in Western Australia. However, in the main, the voyages commenced from the city of Makassar or neighbouring towns to Bira on the south-east coast of South Sulawesi to Selayar, Flores, Alor and Kisar. There they would reprovision and water before the long sea passage to Melville Island, across to the Cobourg Peninsula, Arnhem Land, Groote Eylandt and into the Gulf of Carpentaria.

The vessels used were the traditional type of perahu called the "Padewakang", being anything from 20 to 50 tons or more, using the traditional plaited palm leaf sails, with the crew using the time honoured navigational methods of stars and sun, winds and tides. The voyages commenced with the onset of the north westerly monsoon in November and December. On reaching the north Australian coast, camps were set up, trepang was collected in the shallow bays and processed by boiling, smoke drying and sun drying. As soon as the men had a full cargo, or when the south easterly monsoon set in, in March and April, the ships would return to Makassar and the trepang sold to merchants for the China market.

As would be expected, relationships were established between the Makassan sailors and the Aboriginal communities, and intermarriage took place, descendants of which are living today in a number of towns and outstations on the Arnhem Land coast. As part of the

1988 Australian Bicentenary Commemorations the Historical Society of the Northern Territory proposed a project of historical research, reconstruction of a traditional Makassan perahu and re-enacted voyage to Australia. The project was carried out under the sponsorship of the University of Hasanuddin, Makassar (Dr. Fachruddin, Rector) and the Northern Territory Museum (Dr. C. Jack-Hinton, Director).

In mid-July 1987, the reconstruction of the traditional Makassan perahu 'Padewakang' took place at Tanah Beru, based on my earlier researches and with the advice of Nick Burningham of the Conservation Department of the NT Museum, and sailed from Makassar on 17 December 1987. Thirteen Makassan sailors and myself were on board the *Hati Marege*, as she was named, and sailed to Bira, Selayar, Alor and Kisar for revictualling and watering. From there she sailed to Melville Island and along the Arnhem Land coast to Gove.

On board, as one of the crew of the *Hati Marege* was Mansyur Muhayang Daeng Ngewa, a grandson of Husein Daeng Rangka, a folk hero in the 'dreamtime' of the Yulngu people of Arnhem Land. On landing at Gove and on being introduced to his nephew Matjiwi Burrawanga, great grandson of Yocing (Husein), from Elcho Island, a great family re-union took place and dances of welcome were performed for the crew of the *Hati Marege*. Prior genealogical research had been carried out into the family histories of both the Makassar and Yulngu families and, as a result, direct and living proof of these family relationships were established.

Great ceremonies of welcome were performed and family re-unions took place in Yirrkala, Elcho Island and Milingimbi, and at Elcho Island, Mansyur was initiated into the Irritja family in a highly emotional ceremony.

CURRENT RESEARCH

The *Hati Marege* sailed to Darwin from Gove, stopping at Elcho Island, Milingimbi and Port Essington. After a brief period of rest in Darwin the crew returned to a hero's welcome in Makassar and the *Hati Marege* to a place of honour in the forecourt of the NT Museum of Arts Sciences, Darwin. But the research still goes on. As a result of a grant graciously provided under the Northern Territory Government's History Award Scheme, I was recently enabled to carry out research in Groote Eylandt, in order to establish possible family relations, locate, identify and record Makassan camp sites and other places, and record those stories about the visitors which might survive from times past.

However, no Makassar Warnindilyaugwa relationships were identified from my studies, although stories relating to the visits by the Aboriginal people to Makassar and the Makassar people to Groote Eylandt were recorded (see below). In addition, and very importantly, sites have been identified and recorded on Groote Eylandt, Bickerton and Woodah Islands. The attached map (Fig. 1) indicates the identified sites and provides the Anindilyaugwa place names as well as the Makassar names for those places. Another list on this figure (Fig. 1 last column) provides the English interpretation of those names. Further research is currently planned for other areas of Arnhem Land at Milingimbi, Goulburn and Croker Islands and follow up visits to Yirrkala, Elcho Island and Melville Island. As a result of those researches it is planned to prepare a map of north Australia which will indicate those places visited by the Makassan sailors many years ago and the stories associated with them.

ACKNOWLEDGEMENTS

In this particular work, I wish to thank my informants for their patience and advice: Murabuda Numananga, Natditala Wurramarra (Nadj), Badj, Arangari Wurramarra, Lilina, Jambana Lalara, Bobby Nungumadgbarr, Judith Stokes, Julie Waddy, Susan Fadgeon and the C.M.S. staff and the Council of Angurugu. In addition I would like to thank Richard Herbert, Nambuk Mamrika, Mike Hernies of Umbakumba, Jennifer Baird from Alyangula and my brother Jaymila of Elcho Island. Finally I thank Robin Knox of Darwin and Nurdin Yatim of Makassar.

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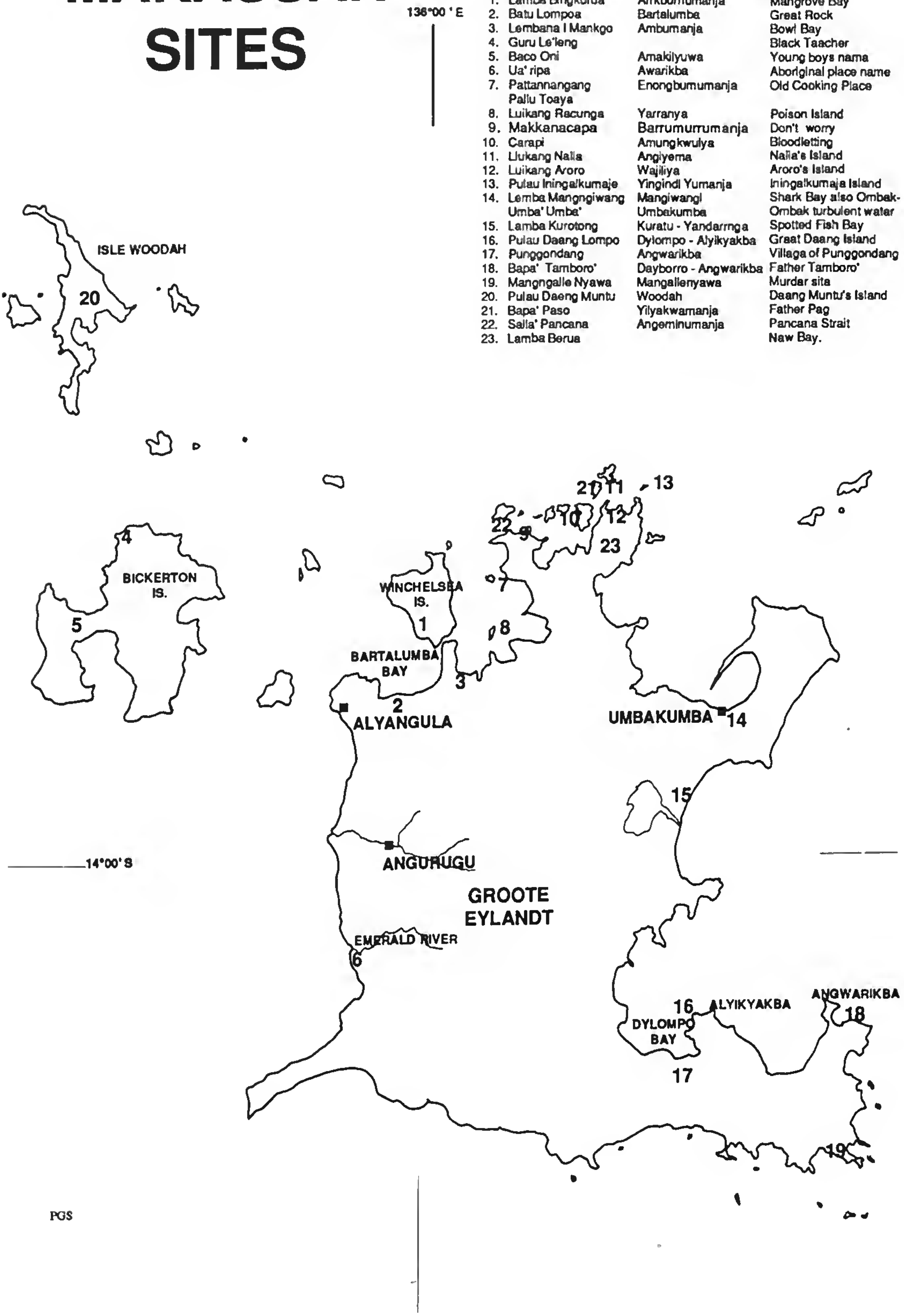
This paper is an abstract of a seminar held in the State Archives, Darwin, 4 July, 1989.

MAKASSAN SITES

MAKASSAR NAME *MANGKASSARA*	ABORIGINAL NAME *ANINDIL YAUGWA*	ENGLISH NAMES
1. Lamba Bingkurua	Arrkburnumanja	Mangrove Bay
2. Batu Lompoa	Bartalumba	Great Rock
3. Lembana I Mankgo	Ambumanja	Bowl Bay
4. Guru Le'leng		Black Teacher
5. Baco Oni	Amakilyuwa	Young boys name
6. Ua' ripa	Awarikba	Aboriginal place name
7. Pattannangang Pallu Toaya	Enongbumumanja	Old Cooking Place
8. Luikang Racunga	Yarranya	Poison Island
9. Makkanacapa	Barrumurrumanja	Don't worry
10. Carapi	Amungkwulya	Bloodletting
11. Llukang Nalla	Angiyema	Nalla's Island
12. Luikang Aroro	Wajiliya	Aroro's Island
13. Pulau Iningalkumaje	Yingindi Yumanja	Iningalkumaja Island
14. Lemba Mangngiwang Umba' Umba'	Mangiwangl Umbakumba	Shark Bay also Ombak-Ombak turbulent water
15. Lamba Kurotong	Kuratu - Yandarrnga	Spotted Fish Bay
16. Pulau Daang Lompo	Dylompo - Alyikyakba	Great Daang Island
17. Punggondang	Angwarikba	Village of Punggondang
18. Bapa' Tamboro'	Dayborro - Angwarikba	Father Tamboro'
19. Mangngalle Nyawa	Mangallenyawa	Murder site
20. Pulau Daeng Muntu	Woodah	Daang Muntu's Island
21. Bapa' Paso	Yilyakwamanja	Father Pag
22. Salla' Pancana	Angeminumanja	Pancana Strait
23. Lamba Berua		Naw Bay.



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BOOK REVIEWS

Charles Darwin in Australia

by F.W. & J.M. Nichols

Cambridge University Press, 1989
Pp. 175, $45.

Clearly, the recent centennial anniversary of Darwin's death has not ended the stream of publications dealing with his life and work, and the present volume provides a welcome addition that both summarizes and illustrates Darwin's Australian connections. The volume briefly introduces H.M.S. *Beagle*, Captain Robert Fitzroy, and many other personalities, and the purposes of the cruise, including the sequence of chronometrical stations at latitudes all round the world, that resulted in the visits of the *Beagle* to Sydney, Hobart and Albany. The *Beagle* arrived in Port Jackson on 11 January 1836 and departed from King George Sound on 14 March, setting course for the Cocos-Keeling Islands. These islands are not included in the present volume although they have been administered by Australia since 1955 and part of the electorate of the Northern Territory since 1984, and were of considerable importance in the formulation of Darwin's views on the development of coral reefs and atolls, described in one of his earlier publications "The Structure and Development of Coral Reefs" (1842), some seventeen years before his magnum opus.

Subsequent chapters describe his journey to Bathurst and his return trip, his impressions of Sydney; his activities in and around Hobart; his visit to King George Sound, with a postscript providing biographies of several of the major participants in Darwin's Australian story, Syms Covington, Conrad Martens, Augustus Earle, J.C. Wickham, Philip P. King, Philip Gidley King and Captain Fitzroy. Appendices provide detailed summaries of the documentary sources relating to Darwin's visit, principally Darwin's field notebooks, diaries, specimen catalogues, abundant correspondence, and the published reports and scientific papers. The volume clearly indicates that Darwin's visit to Australia was not merely as an early tourist, and that he made considerable collections of the fauna of the localities visited, principally of the insects, many of these eventually proving to be species new to science. He also showed great interest in the geology of the regions through which he travelled and kept detailed notes. He certainly experienced much more difficulty in reaching the top of Mount Wellington than the modern tourist, which probably helped to sharpen his observations. He also collected some fossils, a few mammals and reptiles, fishes and even some barnacles, and a planarian flat-worm that also eventually proved to be a new species and was described by Darwin himself in 1844. Of Darwin's insects, 31 of the Sydney species and 48 of the Albany species were new to science. However Darwin's major direct contribution to Australian zoology was made at a later date, in his 1851-54 Ray Society monographs on the Cirripedia (barnacles) where he described 31 new Australian species. These are still the standard reference works at the present time.

Darwin's attitude to things Australian appears to be generally unfavourable, although he clearly prefers Hobart to Sydney, and he finally leaves without regret. No doubt his views were tinged by his homesickness after the lengthy voyage and the failure of his expected mail to arrive in Sydney. It is interesting to imagine how his ideas might have been influenced if his Australian visit had occurred early in the course of the *Beagle*'s voyage instead of near the end. It might also have further influenced his thought if he had visited some localities in tropical Australia, but the *Beagle*, without Darwin, was not to visit the north until its next voyage.

The volume is well produced and reasonably priced and can be recommended to anyone interested in history or science, or both. It is abundantly illustrated, frequently with contemporary paintings, many of which have not been previously reproduced. Unfortunately, several of them are reproduced on too small a

scale, to that they merely decorate the page rather than inform the reader. The panorama of King George Sound is well worth including, for example, but at least at twice the size. One page in the reviewer's copy was also badly stained.

Both Darwin and Captain Fitzroy formed a low opinion of the book sellers that they found in Australia. Perhaps, if their modern counterparts all stock the present volume, the ghosts of Darwin and Fitzroy might be somewhat appeased.

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A Natural History of Domesticated Mammals

Juliet Clutton-Brock

Cambridge University Press 1987 ISBN-0-521-34697-5
British Museum (Natural History) 1987. ISBN 0-565-01050-6.

Pp. 208; RRP.: $27.00 (paperback).

This most interesting volume attempts to explain the nature and origin of mammal domestication. The book has done so by cleverly integrating archaeological information with the products of the prolonged process of domestication that so control our lives today.

The book is introduced by a chapter entitled "Mans place in nature at the end of the ice age". Each of the five sections which follow are subdivided into a series of parts. Thus, section 1 "Man-made animals" has 9 parts; section 2 "Exploited captives" has five parts; section 3 "Small mammals" has 2 parts; section 4 "Exploited ungulates in the pre-Neolithic period" has 1 part as does section 5, "Experimental domestication and game ranching past and present". The conclusions "The geography of domestication" rounds off what is a competently and well-written book.

The volume abounds with illustrations and these take the form of colour photographs (25), black and white photographs (47), line drawings (99) and maps (12). These are well chosen, ideally spaced and impart a simple message in concise format.

The appendices at the end of the book includes a section on the nomenclature of the domestic mammals. This consists of a table defining the taxonomic binomials of domestic mammals and their presumed wild parent species as used in the book (appendix 1). A second appendix includes information on climatic sequences and archaeological divisions of the Quaternary period. Both of these are valuable additions, however, appendix 1 provides us with the first of two criticisms which I wish to make.

Firstly, the author argues that "the now widely accepted premise that names based on descriptions of domestic mammals should not be used for wild species whilst at the same time keeping as close as possible to the traditional nomenclature" (p. 195) should be followed. That is, using the next available name to describe the wild taxa. To me this is a missuse of binomial nomenclature. Scientific names serve two functions, inthat they provide a means of readily distinguishing taxa and they also provide stability for the commonality of names. Many situations exist where names in common usage have been retained

despite their nomenclatorial inexactness. Nevertheless, the author cites as an example of inappropriate nomenclature the domestic water buffalo *Bubalus bubalis* (L). She then assigns as its progenitor the "wild" water buffalo *Bubalus arnee* (Kerr, 1792), even though this species is morphologically indistinguishable from *B. bubalis* and fertile hybrids are formed between the forms. There is no evidence whatsoever to say that *Bubalus arnee* is the wild progenitor to *B. bubalis*, yet this appears to have been assumed by the author. How can *B. arnee* be a progenitor, if it is a separate species? One might expect that progenitors of domesticated stock would be of the same species. The resurrection of this name from taxonomic history can add nothing but confusion to the literature and the nomenclature. *Bubalis arnee* is not a name accepted by taxonomists and it has in the past been placed under the synonomy of *B. bubalis*. For example, the concensus taxonomy of mammals developed in "Mammal species of the world" (Honacki et. al. 1982) does not recognise *B. arnee*. Unfortunately, the author applies such terminology throughout the volume in regard to numerous species.

Secondly, there appears to be a somewhat arbitrary nature in assigning species to either "Man-made animals" or "Exploited captives". Thus, dogs are assigned to the former, whereas cats are assigned to the latter. This decision appears to have been reached on the assumption that many diverse forms of dogs have been created by man's breeding activities, whereas this does not apply so well to cats. Examining some of the more bizarre feline exhibits at a local agricultural show (comparing for example the Russian Blue and the Cornish Rex), suggests that as high a level of genetic manipulation pertains to cats as it does to dogs. The second justification appears to be that house cats can re-adapt to the wild much easier than can dogs and they therefore use man as a convenience. This might be well and true for London, but if the author considers the packs of wild dogs which are found in some Italian cities, or a major problem to sheep farmers in Australia where domestic dogs have gone wild, the arbitrary nature of her decision is highlighted. The point is that many of the inclusions and omissions are arguable.

Nevertheless, despite several aspects which I found irritating, this volume is well put together and well worth reading.

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The Title should be concise and informative and should not include names of new taxa. An abridged title (not exceeding 50 letter spaces) should be included for use as running head.

The Abstract should not exceed 150 words, and should state concisely the scope of the work and give the principal findings.

Keywords, to facilitate information retrieval, of up to 10 in number should be chosen to outline the main subjects covered.

The Introduction, including a review of literature, should not exceed what is necessary to indicate the reason for the work and the essential background. Abbreviations used throughout the text may be explained at the end of the introductory material.

Footnotes are to be avoided, wherever possible, except in papers dealing with historical subjects.

The International System of units should be used.

In the descriptive text numbers from one to nine should be spelt out and figures used for numbers over nine. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Systematic papers must conform with the International Code of Zoological Nomenclature and, as far as possible, with their recommendations.

Synonymies should be given in the short form (*taxon* author, date:page) and the full reference cited at the end of the paper. Full citations of taxa used in the text (i.e. *taxon* author, date) must also be included in the references, whereas the short citation (i.e. *taxon* author) need not be included.

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Tables should be numbered with arabic numerals and accompanied by a title. Horizontal rules are inserted only above and below column headings and at the foot of the table. Footnotes on tables should be kept to a minimum and be reserved for specific items in columns. All other explanatory material should be incorporated with the title.

ILLUSTRATIONS

Line drawings, maps, graphs and photographs are generally regarded as "figures" and are to be numbered consecutively for interspersion through the text. Under special circumstances colour illustrations may be accepted. Drawings must be on drafting film or good quality board with appropriate lettering inserted. Black and white photographs must be sharp, of high contrast on glossy paper, and mounted on board. The author's name, title of paper and figure number must be indicated on the reverse side of all illustrations. Captions or legends should be typed together on pages at the end of the text.

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Citations of sources within the body of the text should include the author, year of publication and page reference (where appropriate), e.g. Roth (1896); (Roth 1896); (Roth 1896, 1898); (Roth 1896; Smith 1915).

References should be arranged alphabetically and chronologically at the end of the paper. Titles of all references must be given in full and wherever possible citations given in BIOSIS format. Where an author has published more than one work referred to in the same year, the references should be appended with the letter (a), (b), etc. The following examples show the style to be followed:

Brake, B., McNeish, J. and Simmons, D. 1979. *Art of the Pacific*. Oxford University Press: Wellington.

Cogger, H.G. 1981. A Biogeographic Study of the Arnhem Land Herpetofauna. In: *Proceedings of the Melbourne Herpetological Symposium:* 148-155. Zoological Board of Victoria: Melbourne.

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